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Natural regeneration in tree islands drives long-term recovery of native forest-associated woody species in oil palm landscapes (Sumatra, Indonesia)

MASTER THESIS

by

Vivien Michel
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in Düren, Germany

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Abstract

1. Large-scale conversion of tropical rainforest to oil palm plantations is a major driver of biodiversity loss in Southeast Asia, particularly threatening native forest-associated woody species and their associated biota. Integrating tree islands within monocultural oil palm landscapes has emerged as a promising approach to enhance native biodiversity. However, the effectiveness of such interventions in sustaining natural regeneration and long-term recovery of native woody species remains unclear.
2. Using a large-scale biodiversity enrichment experiment of 52 tree islands varying in size (25 m^2 to 1600 m^2) and planted tree diversity (0, 1, 2, 3, and 6 species) embedded within a conventional oil palm plantation in Sumatra since 2013, I analyzed temporal trajectories in the diversity and abundance of naturally recruiting woody species based on four complete censuses conducted between four and ten years (2018 – 2024) after natural regeneration began.
3. Across all censuses, 82 recruiting woody species (trees and shrubs) were recorded, representing 64 genera and 34 families. At the landscape (gamma) scale, species richness and abundance increased by ~42% and ~69%, respectively, from 2018 to 2024, accompanied by shifts in community evenness and continued arrival of locally rare species. After ten years, neither richness nor abundance showed signs of saturation, indicating ongoing accumulation of recruiting species.
4. Tree islands consistently favored natural regeneration of native diversity, with 90 % of recruiting species and individuals being native. Native forest-associated species (N=35 across years) increased steadily at landscape scale, while localized dominance of alien species did not indicate successional arrest.
5. At the local (alpha) scale, larger tree island area exerted and sustained a positive effect on recruiting diversity, and higher initial planted tree diversity promoted native recruitment, and in particular native forest-associated recruiting species, at earlier stages, although this effect diminished over time.
6. *Synthesis and applications.* Tree islands enhance natural regeneration and accelerate the recovery of native forest-associated woody diversity over extended time periods, providing an effective strategy for conserving tropical forest biodiversity within oil palm landscapes. However, preserving primary forests, irreplaceable reservoirs of native forest-associated species, remain essential for supporting continued recruitment into tree islands and maintaining their function as stepping-stone habitats.

***Keywords**:* natural regeneration, tree islands, succession, restoration, alien species, enrichment planting, tree diversity experiment, sustainable oil palm, Indonesia

1 Introduction

Southeast Asian and Sumatran lowland rainforests are unique centers of biodiversity (Myers et al., 2000; Pillay et al., 2022; Cai et al., 2023). Sumatran forests are part of the Sundaland biodiversity hotspot, where exceptionally high rates of endemism are found (Myers et al., 2000; Cai et al., 2023), harboring about 25,000 vascular plant species, of which 15,000 are endemic (Brooks et al., 2000). Thirty-one percent of the Sumatran flora is endemic to the island (Sun et al., 2024), with most of this diversity concentrated in lowland forests that also support many forest-dependent species (CEPF, 2001; Rembold et al., 2017). Yet, these forests have undergone rapid deforestation and significant biodiversity loss in recent decades, primarily driven by the expansion of oil palm plantations (Rembold et al., 2017; Qaim et al., 2020; Gaveau et al., 2022; Ke et al., 2025). Over the past three decades, Indonesia has shown the highest overall rate of agricultural expansion and associated forest loss in Southeast Asia (Ke et al., 2025). A quarter of all primary forest loss between 2001 and 2019 occurred in Sumatra (Gaveau et al., 2022). The expansion of both industrial and smallholder oil palm plantations remains a dominant driver of deforestation (Qaim et al., 2020), with at least one third of the country's old-growth forest loss in this period attributed to oil palm plantations (Gaveau et al., 2022). Such land-use change is associated with a significant reduction in local and regional biodiversity and ecosystem functioning (Foster et al., 2011; Clough et al., 2016; Dislich et al., 2016; Drescher et al., 2016; Rembold et al., 2017; Kusuma et al., 2018). At broader spatial scales, these shifts are compounded by the proliferation of alien species, a major driver of biodiversity loss in the tropics (Mungi et al., 2025), which contributes to the homogenization of species-rich communities and transforms lowland oil palm landscapes from native- to alien-dominated plant assemblages (Dornelas et al., 2014; Rembold et al., 2017; Kusuma et al., 2018; Fricke and Svenning, 2020). This highlights an urgent need to recover native biodiversity within these agricultural landscapes. On the other hand, oil palm expansion has also socioeconomic benefits, including increased employment, improved access to education and rural income, and poverty reduction among farmers and workers (Drescher et al., 2016; Qaim et al., 2020). Thus, alongside efforts to safeguard remaining forests (Jones et al., 2018; Watson et al., 2018; Gaveau et al., 2022; Struebig et al., 2025), there is a critical need to identify economically viable approaches for restoring biodiversity within ecologically simplified oil palm landscapes (Clough et al., 2016; Grass et al., 2019; Holl et al, 2020; Qaim et al., 2020; Brancalion et al., 2025).

A continuum of ecological restoration approaches is increasingly considered to enhance native biodiversity in human-modified tropical landscapes (Chazdon et al., 2021), ranging from natural regeneration alone to progressively higher levels of intervention such as enrichment planting and large-scale tree planting. Their suitability depends on previous land-use intensity, current site degradation, landscape integrity, and the social and ecological objectives (Chazdon and Guariguata, 2016; Jones et al., 2018; Poorter et al., 2023). Natural regeneration minimizes disturbance and can create species-rich secondary forests (Norden et al., 2009; Van Breugel et al., 2013; Chazdon and Guariguata, 2016; Rozendaal et al., 2019), but its success is often limited by distance to forest remnants, seed availability, and the scarcity of dispersers in fragmented landscapes (Zahawi and Augspurger, 2006; Norden et al., 2009; Chazdon and Guariguata, 2016; Rozendaal et al., 2019; Bardino et al., 2023; Poorter et al., 2023). Invasive species can further hinder natural regeneration (Matos et al., 2022¸ Poorter et al., 2023). In contrast, large-scale tree planting can accelerate succession by rapidly providing shade, improving microclimatic conditions, and facilitating the establishment of shade-tolerant and later-successional species (Brancalion et al., 2025; Holl et al., 2020; Poorter et al., 2023). Tree islands, i.e. clusters of native trees planted within agricultural or degraded landscapes, have emerged as a promising and cost-effective restoration strategy (Zahawi et al., 2013; Holl et al., 2020). They can counteract several limitations of natural regeneration by acting as small regeneration nuclei that follow the nucleation model of succession, enhancing natural recruitment and accelerating recovery through improved seed dispersal and more favorable microclimatic conditions for later-successional species (Zahawi et al., 2013; Poorter et al., 2023; Brancalion et al., 2025; Song et al., 2025). Tree islands may also increase landscape connectivity by functioning as stepping-stone habitats (Uezu et al., 2008; Saura et al., 2014; Arroyo-Rodríguez et al., 2020). Compared with full restoration plantings, tree islands and natural regeneration are highly cost-efficient and feasible at large scales (Chazdon and Guariguata, 2016; Jones et al., 2018), while delivering comparable benefits for biodiversity and ecosystem functioning (Zahawi and Augspurger, 2006; Zahawi et al., 2013; Crouzeilles et al., 2017; Meli et al., 2017; Holl et al., 2020; Banin et al., 2022; Zemp et al., 2023; Paterno et al., 2024; Joyce et al., 2025). Nonetheless, most existing evidence comes from short-term studies which focus on the first five years of recovery, highlighting the need for analyzing recruitment dynamics and restoration trajectories over longer time frames (Meli et al., 2017; Brancalion et al., 2025).

Restoration through natural regeneration is a long-term process driven by multiple interacting factors that govern community assembly and diversity. Evidence indicates that community assembly can be influenced by design choices, including planted tree diversity and species composition (Paterno et al., 2024; Piquer-Doblas et al., 2024; Brancalion et al., 2025). Within the tree island systems approach, island size is a key feature, as larger areas typically support more species due to higher colonization probabilities and lower extinction risks for recruiting species (species-area relationship (Arrhenius et al., 1921); MacArthur and Wilson, 1967; Rosenzweig, M., 2003). The optimal tree island configuration (i.e., island size and planted tree diversity) for maximizing biodiversity recovery at both local and landscape scales remains unresolved (Zahawi et al., 2013; Holl et al., 2020; Zemp et al., 2023; Paterno et al., 2024), and how the influence of initial restoration design shifts over time is still poorly understood. Forest ecosystems under restoration typically show rising taxonomic diversity over time, especially when disturbance-tolerant pioneer species overlap with shade-tolerant, later-successional species (Van Breugel et al., 2013; Vellend et al., 2013; Rozendaal et al., 2019; Van der Sande et al., 2024). As vegetation structure develops, conditions become more favorable for later-successional species, and increasing habitat heterogeneity promotes niche complementarity, further boosting diversity (Poorter et al., 2023; Van der Sande et al., 2024). Seed dispersal and the regional species pool also influence community assembly and diversity (DeFilippis et al., 2024). While pioneer species often are dispersed by wind or bats, long-distance dispersal by birds and mammals is essential for the recruitment of later-successional species, supporting continued diversity gains (Zahawi and Augspurger, 2006; Poorter et al., 2023; Piquer-Doblas et al., 2024). Conversely, increasing competitive exclusion during vegetation build-up may counteract these gains (Poorter et al., 2023; Van der Sande et al., 2024), particularly where alien invasive pioneer species suppress the establishment of later-successional species (Vellend et al., 2013; Poorter et al., 2023).

Alien species can cause arrested succession, in which tree regeneration is suppressed over extended periods (Royo and Carson, 2006). Their rapid establishment, fast growth, and persistence in disturbed open habitats (D'Antonio and Meyerson, 2002; Gioria et al., 2023; Poorter et al., 2023) allow dominant alien species to alter community structure and ecosystem processes, substantially constraining the recovery of ecosystems and native diversity (D'Antonio and Meyerson, 2002; Pearson et al., 2018; Weidlich et al., 2020; Matos et al., 2022). For example, in the Brazilian Atlantic forest, in a study by Matos et al. (2022) comparing tree diversity recovery between Acacia-invaded and non-invaded second-growth forests, invaded forests exhibited markedly lower taxonomic diversity and endemic species abundance, with no increase in diversity over time compared to non-invaded forests. Therefore, understanding how restoration actions shape the long-term recovery of native and alien diversity is essential for improving restoration effectiveness in tropical landscapes and reducing the risk of arrested succession. Recovering native forest-associated woody diversity is a priority in restoration, as remaining lowland forests, key reservoirs of native forest-dependent biodiversity (Rembold et al., 2017), are increasingly fragmented and highly vulnerable to plant invasions and other pressures from deforestation and land-use change (Rembold et al., 2017; Mungi et al., 2021; Gaveau et al., 2022; Mungi et al., 2025). Within plantation landscapes, management practices such as weeding, fertilization, and herbicide application, as well as high open canopies and hot, dry microclimates exclude most forest-dependent plant species (Rembold et al., 2017), leading to declines in native forest-associated woody species and corresponding losses of forest-dependent fauna (Foster et al., 2011; Rembold et al., 2017). The maintenance of specialist interactions and a forest's biotic resistance to invasion further relies on sustaining native diversity (Pyšek et al., 2012; Mungi et al., 2025). Hence, native forest-associated species are central targets in tropical restoration (e.g. Cole et al., 2010; Gilman et al., 2016; Lu et al., 2017; Paterno et al., 2024; Simões et al., 2024). A key remaining knowledge gap is to develop cost-effective restoration strategies capable of restoring woody diversity in oil palm landscapes over time, providing refugia for native forest-associated species, and limiting invasion by alien plants. Addressing this gap requires long-term monitoring to track restoration trajectories (Weidlich et al., 2020; Mungi et al., 2025).

In this study, I analyze the temporal trends (2018-2024) in the taxonomic diversity and abundance of native forest-associated and alien naturally recruiting woody species within the EFForTS-BEE experiment (Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems: Biodiversity Enrichment Experiment; Rembold et al., 2017). This large-scale biodiversity enrichment experiment comprises 52 tree islands embedded in an industrial-scale oil palm plantation in Sumatra since 2013 (Teuscher et al., 2016). The tree islands systematically vary in size (25, 100, 400, 1600 m^2) and planted tree diversity (0, 1, 2, 3, or 6 native species). Four complete censuses of the naturally recruiting woody plants, hereafter referred to as recruiting diversity, were conducted in the tree islands between four and ten years after the onset of natural regeneration. This study addresses two main questions: **1. Landscape-scale recruitment dynamics in the tree islands**: How do the diversity and abundance of naturally recruiting woody species change over time, and to what extent do tree islands foster the return of native forest-associated species while limiting the dominance of alien species at landscape (gamma) scale? I expect overall recruiting diversity and abundance to increase over time at landscape scale (H1), driven by cumulative seed arrival and vegetation development. A steady rise is expected if long-distance seed dispersal by animals is an important mechanism in the study region; saturation may occur if the regional species pool is limited; and a slight decline could result from competitive exclusion, such as suppression of native recruitment by dominant alien species. Native forest-associated recruiting diversity is expected to show a delayed but sustained increase (H2), reflecting initially slow establishment and more favorable, shaded conditions in later-successional stages. In contrast, alien species, with rapid early colonization and a smaller regional species pool, are expected to reach saturation of diversity earlier (H3). **2. Local-scale effects of restoration treatments**: How do initial tree island area and planted tree diversity influence temporal changes in local (alpha) recruiting diversity, particularly of native forest-associated species? I hypothesize that larger tree island areas enhance recruiting diversity, including native forest-associated diversity, with effects strengthening over time (H4) due to the species-area relationship, reduced edge effects, and greater microhabitat heterogeneity, promoting the establishment of disturbance-sensitive later-successional species. Higher planted tree diversity is expected to initially increase recruiting diversity, and in particular native forest-associated diversity, by creating more heterogeneous conditions. Over time, however, this effect may diminish as natural recruitment creates more complex vegetation structure within tree islands. Resulting converging light and microclimatic conditions between tree islands regardless of planted tree diversity are expected to decrease the initial planted-diversity driven differences in recruiting diversity (H5).

2 Methods

2.1 Study region

The study was conducted in the EFForTS-BEE experiment (Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems: Biodiversity Enrichment Experiment) located near Bungku village, Jambi, Sumatra, Indonesia (01.95◦ S and 103.25◦ E, 47 ± 11 m a.s.l.). The region was formally dominated by dipterocarp-dominated lowland rainforest that had been transformed into conventional oil palm plantations (Laumonier et al., 2010; Teuscher et al., 2016). The surrounding landscape is dominated by oil-palm plantations (83% in 2016), with smaller areas of secondary forest (4% in 2016), rubber cultivation (2% in 2016), fallow land (6% in 2016), bare soil (5% in 2016), as well as orchards, water bodies and urban infrastructure (<1% in 2016) (Khokthong, 2019). The linear distance to the nearest forest, Hutan Harapan, is roughly 18 km. The climate is humid tropical, with a mean temperature of 26.7 °C and an annual rainfall of 2235 mm, marked by two rainfall peaks around March and December and a drier period during July to August (Drescher et al., 2016). Loamy Acrisol soils constitute the predominant soil type in the region (Allen et al., 2015).

2.2 Experimental design

The EFForTS-BEE experiment was established in 2013 within a 140-ha industrial oil palm plantation of PT. Humusindo Makmur Sejati (Teuscher et al., 2016; Zemp et al., 2023). Oil palms had been planted in a 9x9 triangular grid between 2001 and approximately 2007, with ca. 143 oil palms per ha (Teuscher et al., 2016). The conventional management of the plantation includes fertilizer application, manual weeding and removal of epiphytes, with rare application of herbicides (Teuscher et al. 2016). The plantation is also used for livestock farming (Teuscher et al., 2016). The EFForTS-BEE experiment is part of the global network of tree diversity experiments (TreeDivNet; Paquette et al. 2018).

A total of 52 tree islands were established within the oil palm plantation in December 2013, systematically varying in size (25, 100, 400, 1600 m²) and levels of planted tree diversity (0, 1, 2, 3, or 6 species), following the random partitions design (Bell et al. 2009). Natural regeneration was allowed within the tree islands (see Figure S1; Teuscher et al., 2016; Zemp et al., 2023). The minimum distance between tree islands was 85 m.

Within each tree island, native trees were planted in a 2 m - grid among oil palms. To improve light availability for planted trees, approximately 40% of oil palms were removed, except in the 5 x 5 m islands that were positioned between existing oil palm rows. Six native multi-purpose species were used: *Parkia speciosa* Hassk. (Fabaceae), *Archidendron jiringa* (Jack) I.C. Nielson (Fabaceae) and *Durio zibethinus* L. (Malvaceae) that are mainly grown for fruits, *Peronema canescens* Jack (Lamiaceae) and *Shorea leprosula* Miq. (Dipterocarpaceae) used for timber, and *Dyera polyphylla* (Miq.) Steenis (Apocynaceae) that produces natural latex (Teuscher et al., 2016; Paterno et al., 2024). In total, 6354 trees were planted across tree islands (Teuscher et al., 2016). After planting, no fertilizers, herbicides or pesticides were applied within the tree islands anymore (Teuscher et al., 2016). One year after establishment, weed control was stopped to promote natural regeneration (Teuscher et al., 2016; Paterno et al., 2024). Further methodological details are provided in Teuscher et al. (2016).

2.3 Data collection

All experimental plots were fully censused for naturally regenerating woody plants from four to ten years after the onset of natural regeneration in 2014. Censuses were conducted in 2018 (April-August), 2020 (October-December), 2022 (June-October) and 2024 (August-November).

The survey included trees, shrubs, bamboos and lianas - the latter consistently recorded only in 2024 - with a minimum height of 130 cm. Recruiting oil palms were included with a minimum stem diameter of 10 cm. All recorded individuals were tagged uniquely and when still alive resurveyed across census years. Species identification was carried out to species level, with only a few exceptions - *Secamone sp*., *Syzygium sp*., *Ixora sp*. and *Nephelium sp.* were identified to genus level. Identification was based on field photographs and collected voucher specimens, supported by relevant floras (Flora Malesiana, Tree Flora of Malaya, Flora of the Malay Peninsula) and databases (Plants of the World Online, Digital Flora of Indonesia), as well as taxonomic monographs and revisions where necessary. For each species, lifeform (tree, treelet, shrub, liana) and habitat (forest-associated, open-habitat-associated) were assigned using the same databases. Species were classified as native or alien to Sundaland using Plants of the World Online (2025).

For each recorded individual, total height, stem diameter at 10 cm (d10) and stem diameter at 130 cm (dbh) were measured, and the exact position within the tree island was recorded.

Further details about the field inventory and associated measurements are provided in the field protocol (Appendix 1).

2.4 Data analysis

Prior to analysis, data from the four separate censuses were cleaned, standardized, and synchronized in terms of species identification, allowing for accurate temporal comparisons of recruiting diversity. Excluded from the temporal analysis were all liana species - as consistently recorded only in 2024 - and non-woody species except for recruiting oil palms (Table 1 in Appendix 2). Further, individuals without species identification, dead individuals, and stems that vegetatively reproduced from planted trees were not included. After careful verification, 24 individuals - documented in the censuses prior to and after 2022 but absent from the 2022 dataset - were incorporated into the 2022 data. For further full details on data processing, please refer to the data processing protocol (Appendix 2).

To estimate diversity at the local tree island (alpha) and landscape (gamma) scales, I used the Hill numbers framework (Chao et al., 2021), which quantifies taxonomic diversity as the effective number of species, while the parameter q defines how strongly the measure gives weight to the relative abundance of species. In this framework, q = 0 corresponds to species richness, q = 1 reflects the effective number of common or abundant species (based on Shannon entropy), and q = 2 describes the effective number of dominant or highly abundant species (inverse of the Simpson concentration index) (Chao et al., 2021).

Hill diversity was calculated for q orders 0, 1, and 2 using the *iNEXT.3D* package (Chao et al., 2021). Taxonomic diversity was estimated for five subsets: (i) all species, (ii) native species, (iii) native forest-associated species, (iv) native open-habitat-associated species, and (v) alien species, at both landscape and local scales for each survey year (2018, 2020, 2022, 2024).

Pielou’s evenness was calculated with the *diversity* function in the R package *vegan* (Oskanen et al., 2025). To test temporal differences in community composition at the plot scale across the four survey years, I computed a dissimilarity matrix using the *vegdist* function and tested for differences among years with a permutation-based analysis of variance using *adonis2*.

To test the experimental effects of tree island area and planted tree diversity on local recruiting diversity over time, I fitted linear mixed models (LMMs) for the three focal subsets of native, native forest-associated, and alien species at the local scale. The two continuous variables tree island area and planted tree diversity, plus year as categorical variable, were included as fixed effects. Interaction terms between year and planted tree diversity, and between year and tree island area, were added to test for time-dependent effects on recruiting diversity. Tree island ID was included as a random effect to account for repeated measurements and avoid pseudoreplication. Models were fitted using the *glmmTMB* function from the R package *glmmTMB* (Brooks et al., 2017). Fixed effects significance was evaluated with the Wald Chi-square test (type III sum of squares), using the *Anova* function in the R package *car* (Fox and Weisberg, 2019). Model predictions were visualized with the *ggpredict* function from R package *ggeffects (*Lüdecke, 2018). To compare fixed effects across the three subsets and q orders, I generated a multi-model forest plot using the *plot_models* function from R package *sjPlot* (Lüdecke, 2025). The response variable, recruiting diversity, was log-transformed (log(x+1)) for each subset to improve model residuals. The predictors tree island area and planted tree diversity were log-transformed and scaled. For model validation and residual diagnostics, I used the *check_model* function from the R package *performance*. For all statistical tests, a significance level of p-value < 0.05 was used.

All analyses were performed in R version 4.4.1 (R Core Team, 2024). Data cleaning and calculations were performed under the framework of the R package *tidyverse* (Wickham et al., 2019). Figures were created using the R packages *ggplot2* (Wickham, 2016) and *patchwork* (Pedersen, 2025), next to *ggeffects* (Lüdecke, 2018) and *sjPlot* (Lüdecke, 2025) as outlined.

3 Results

3.1 Overview

The dataset comprised 12,829 records of naturally regenerated woody individuals, collected across four censuses (2018, 2020, 2022, 2024), including resurveyed individuals. Across surveys, I found a total of 82 different woody species (Table 1, excluding lianas) among ~8,237 identified individuals that established within the tree islands, representing 64 genera from 34 plant families. Additionally, woody lianas comprised 28 species recorded in 2024 (Table S1) but were excluded from the temporal analyses.

The number of recruiting individuals, species, genera, and families increased over time (Figure 1). The most species-rich families throughout the years were Moraceae (N = 12), Euphorbiaceae (N= 10), and Rubiaceae (N = 8), and species richness within these families increased over time.

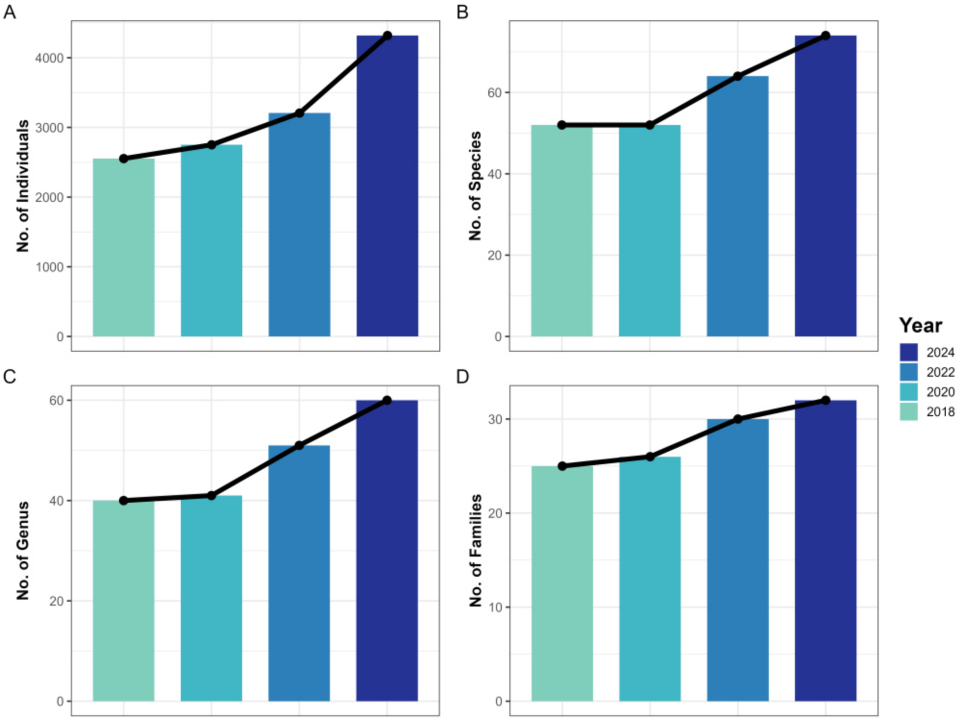

Figure 1: Numbers of recorded individuals (A), species (B), genera (C), and families (D) over the four complete inventories (2018, 2020, 2022, 2024) of recruiting diversity.

The great majority of recruiting species were native (90%, N = 74), as were 90 % of recorded individuals. Thirty-seven species (46 %) were forest-associated, 35 of which were native. Only two of eight recorded alien species were forest-associated (*Swietenia macrophylla* King (Meliaceae), *Artocarpus heterophyllus* Lam. (Moraceae)).

Table 1: List of all recruiting woody species recorded between 2018 and 2024, with respective lifeform, origin, habitat, 2018-2024 occurrences and tree island occupancy in 2024 (i.e. percentage of tree islands in which the species was present). Families and their respective species are listed in alphabetical order.

Family	Species	Origin	Lifeform	Habitat	2018	2020	2022	2024	Occupancy 2024 (%)
Annonaceae	*Polyalthia cauliflora* Hook.f. & Thomson	native	tree	forest	0	0	1	1	1.92
Apocynaceae	*Alstonia angustiloba* Miq.	native	tree	forest	40	66	71	80	50
Apocynaceae	*Tabernaemontana pauciflora* Blume	native	treelet	forest	6	22	21	33	23.08
Arecaceae	*Elaeis guineensis* Jacq.	alien	tree	open	0	76	116	139	46.15
Asteraceae	*Clibadium surinamense* L.	alien	shrub	open	21	6	1	0	0
Cannabaceae	*Trema tomentosum* (Roxb.) H.Hara	native	tree	open	65	12	1	0	0
Combretaceae	*Terminalia cf. calamansanai* (Blanco) Rolfe	native	tree	open	1	1	1	1	1.92
Dilleniaceae	*Dillenia cf. excelsa* (Jack) Martelli ex Gilg.	native	tree	forest	6	11	11	16	3.85
Dipterocarpaceae	*Hopea sangal* Korth.	native	tree	forest	0	0	1	1	1.92
Elaeocarpaceae	*Elaeocarpus cf. stipularis* Blume	native	tree	forest	0	0	1	2	3.85
Euphorbiaceae	*Croton argyratus* Blume	native	tree	forest	6	10	16	25	19.23
Euphorbiaceae	*Macaranga aff. conifera* (Rchb.f. & Zoll.) Müll.Arg.	native	tree	forest	15	10	14	15	15.38
Euphorbiaceae	*Macaranga bancana* (Miq.) Müll.Arg.	native	tree	open	1	1	6	17	15.38
Euphorbiaceae	*Macaranga gigantea* (Rchb.f. & Zoll.) Müll.Arg.	native	tree	open	2	1	1	2	3.85
Euphorbiaceae	*Macaranga hosei* King ex Hook.f.	native	tree	open	1	0	0	0	0
Euphorbiaceae	*Macaranga trichocarpa* (Zoll.) Müll.Arg.	native	shrub	open	1002	775	736	526	48.08
Euphorbiaceae	*Mallotus macrostachyus* (Miq.) Müll.Arg.	native	tree	open	3	4	3	4	3.85
Euphorbiaceae	*Mallotus paniculatus* (Lam.) Müll.Arg.	native	tree	open	2	2	2	0	0
Euphorbiaceae	*Mallotus peltatus* (Geiseler) Müll.Arg.	native	tree	open	7	10	27	67	21.15
Euphorbiaceae	*Triadica cochinchinensis* Lour.	native	tree	open	0	0	0	1	1.92
Fabaceae	*Archidendron jiringa* (Jack) I.C.Nielsen	native	tree	forest	1	1	1	11	5.77
Fabaceae	*Dalbergia junghuhnii* Benth.	native	treelet	open	0	0	0	1	1.92
Fabaceae	*Peltophorum dasyrhachis* (Miq.) Kurz	native	tree	forest	0	0	0	1	1.92
Fabaceae	*Senna alata* (L.) Roxb.	alien	shrub	open	9	14	5	10	1.92
Hypericaceae	*Cratoxylum formosum* (Jack) Benth. & Hook.f. ex Dyer	native	tree	forest	2	3	2	2	3.85

Hypericaceae	*Cratoxylum sumatranum* (Jack) Blume	native	tree	forest	0	0	3	3	3.85
Lamiaceae	*Callicarpa pentandra* Roxb.	native	tree	open	1	0	0	0	0
Lamiaceae	*Clerodendrum disparifolium* Blume	native	tree	forest	17	21	28	46	21.15
Lamiaceae	*Peronema canescens* Jack.	native	tree	open	123	296	343	455	34.62
Lamiaceae	*Vitex quinata* (Lour.) F.N.Williams	native	tree	forest	21	36	33	40	21.15
Lauraceae	*Litsea cf. robusta* Blume	native	tree	forest	0	0	2	3	3.85
Lauraceae	*Litsea umbellata* (Lour.) Merr.	native	tree	open	1	3	14	48	34.62
Malvaceae	*Commersonia bartramia* (L.) Merr.	native	tree	open	1	1	1	1	1.92
Malvaceae	*Hibiscus macrophyllus* Roxb. ex Hornem.	native	tree	open	9	11	11	14	13.46
Malvaceae	*Trichospermum javanicum* Blume	native	tree	forest	1	0	0	0	0
Malvaceae	*Urena lobata* L.	native	shrub	open	1	0	1	2	1.92
Melastomataceae	*Bellucia pentamera* Naudin	alien	tree	open	1	16	5	6	1.92
Melastomataceae	*Melastoma malabathricum* L.	native	shrub	open	661	232	216	235	40.38
Melastomataceae	*Pternandra azurea* (Blume) Burkill	native	tree	open	0	0	1	2	1.92
Meliaceae	*Swietenia macrophylla* King	alien	tree	forest	5	171	214	347	23.08
Moraceae	*Artocarpus dadah* Miq.	native	tree	forest	0	0	1	1	1.92
Moraceae	*Artocarpus heterophyllus* Lam.	alien	tree	forest	0	0	0	1	1.92
Moraceae	*Artocarpus limpato* Miq.	native	tree	forest	0	0	0	1	1.92
Moraceae	*Ficus aurata* (Miq.) Miq.	native	treelet	open	4	4	3	16	5.77
Moraceae	*Ficus caulocarpa* (Miq.) Miq.	native	tree	forest	1	2	2	4	7.69
Moraceae	*Ficus cf. padana* Burm.f.	native	tree	open	0	1	1	0	0
Moraceae	*Ficus dimorpha* King	native	treelet	forest	270	414	456	319	69.23
Moraceae	*Ficus glandulifera* (Wall. ex Miq.) King	native	tree	forest	4	2	3	2	3.85
Moraceae	*Ficus grossularioides* Burm.f.	native	tree	open	1	0	0	0	0
Moraceae	*Ficus variegata* Blume	native	tree	open	5	11	11	5	7.69
Moraceae	*Ficus vrieseana* Miq.	native	tree	open	1	9	13	25	13.46
Moraceae	*Sloetia elongata* (Miq.) Koord.	native	tree	open	1	1	3	3	5.77
Myrtaceae	*Syzygium sp.VM0002*	native	tree	NA	0	0	0	3	3.85
Opiliaceae	*Champereia manillana* (Blume) Merr.	native	treelet	forest	0	2	2	2	3.85
Pandaceae	*Galearia filiformis* (Blume) Boerl.	native	treelet	forest	0	1	2	5	5.77
Pandaceae	*Microdesmis caseariifolia* Planch.	native	treelet	forest	3	9	13	13	17.31

Pentaphylacaceae	*Eurya nitida* Korth.	native	treelet	open	1	1	1	1	1.92
Phyllanthaceae	*Aporosa benthamiana* Hook.f.	native	tree	forest	0	0	1	1	1.92
Phyllanthaceae	*Aporosa octandra* (Buch.-Ham. ex D.Don) Vickery	native	tree	open	0	0	0	1	1.92
Phyllanthaceae	*Baccaurea brevipes* Hook.f.	native	treelet	forest	0	0	1	2	3.85
Phyllanthaceae	*Breynia racemosa* (Blume) Müll.Arg.	native	treelet	open	9	23	14	47	25
Phyllanthaceae	*Bridelia glauca* Blume	native	tree	forest	0	1	1	2	3.85
Phyllanthaceae	*Glochidion borneense* (Müll.Arg.) Boerl.	native	tree	open	1	0	1	2	3.85
Poaceae	*Gigantochloa scortechinii* Gamble	native	shrub	open	0	193	134	113	26.92
Rhizophoraceae	*Carallia brachiata* (Lour.) Merr.	native	tree	forest	0	0	0	1	1.92
Rhizophoraceae	*Gynotroches axillaris* Blume	native	tree	open	0	0	2	2	1.92
Rubiaceae	*Adina eurhyncha* (Miq.) Å.Krüger & Löfstrand	native	tree	forest	0	0	0	2	3.85
Rubiaceae	*Canthium horridum* Baill.	native	shrub	open	3	7	8	8	7.69
Rubiaceae	*Eumachia cf. montana* (Blume) I.M.Turner	native	shrub	forest	0	1	4	9	11.54
Rubiaceae	*Ixora sp.VM0025*	native	shrub	NA	0	0	0	1	1.92
Rubiaceae	*Neolamarckia cadamba* (Roxb.) Bosser	native	tree	open	1	1	1	1	1.92
Rubiaceae	*Neonauclea calycina* (Bartl. ex DC.) Merr.	native	tree	open	4	7	9	23	13.46
Rubiaceae	*Psychotria viridiflora* Reinw. ex Blume	native	shrub	forest	0	0	0	5	7.69
Rubiaceae	*Urophyllum peltistigma* Miq.	native	treelet	forest	0	3	3	4	5.77
Rutaceae	*Clausena excavata* Burm.f.	native	tree	open	1	12	17	44	30.77
Salicaceae	*Homalium caryophyllaceum* (Zoll. & Moritzi) Benth.	native	treelet	forest	2	2	2	3	1.92
Sapindaceae	*Nephelium sp.DMF0033*	native	tree	forest	36	104	128	208	30.77
Simaroubaceae	*Brucea javanica* (L.) Merr.	native	treelet	open	1	0	0	1	1.92
Solanaceae	*Solanum jamaicense* Mill.	alien	shrub	open	74	24	38	22	32.69
Strombosiaceae	*Strombosia ceylanica* Gardner	native	tree	forest	0	0	0	1	1.92
Verbenaceae	*Stachytarpheta australis* Moldenke	alien	shrub	open	24	0	0	2	3.85
Vitaceae	*Leea javanica* Blume	native	tree	open	74	104	421	1256	51.92

3.2 Temporal changes in recruiting diversity and abundance

From 2018 to 2024, I found a 42 % increase in species richness at landscape scale ($S_{2018} = 52$, $S_{2024} = 74$), while seven more families were added. Recruiting abundance increased by 69 % ($N_{2018} = 2553$, $N_{2024} = 4319$). For both species richness ($q = 0$) and richness of common species ($q = 1$), rarefaction curves showed increases over time (Figure 2A). The extrapolated asymptotic estimate for 2024 was 83.5 species ($q = 0$), exceeding the observed species richness ($S_{2024} = 74$), and indicating non-saturation of landscape-scale species richness.

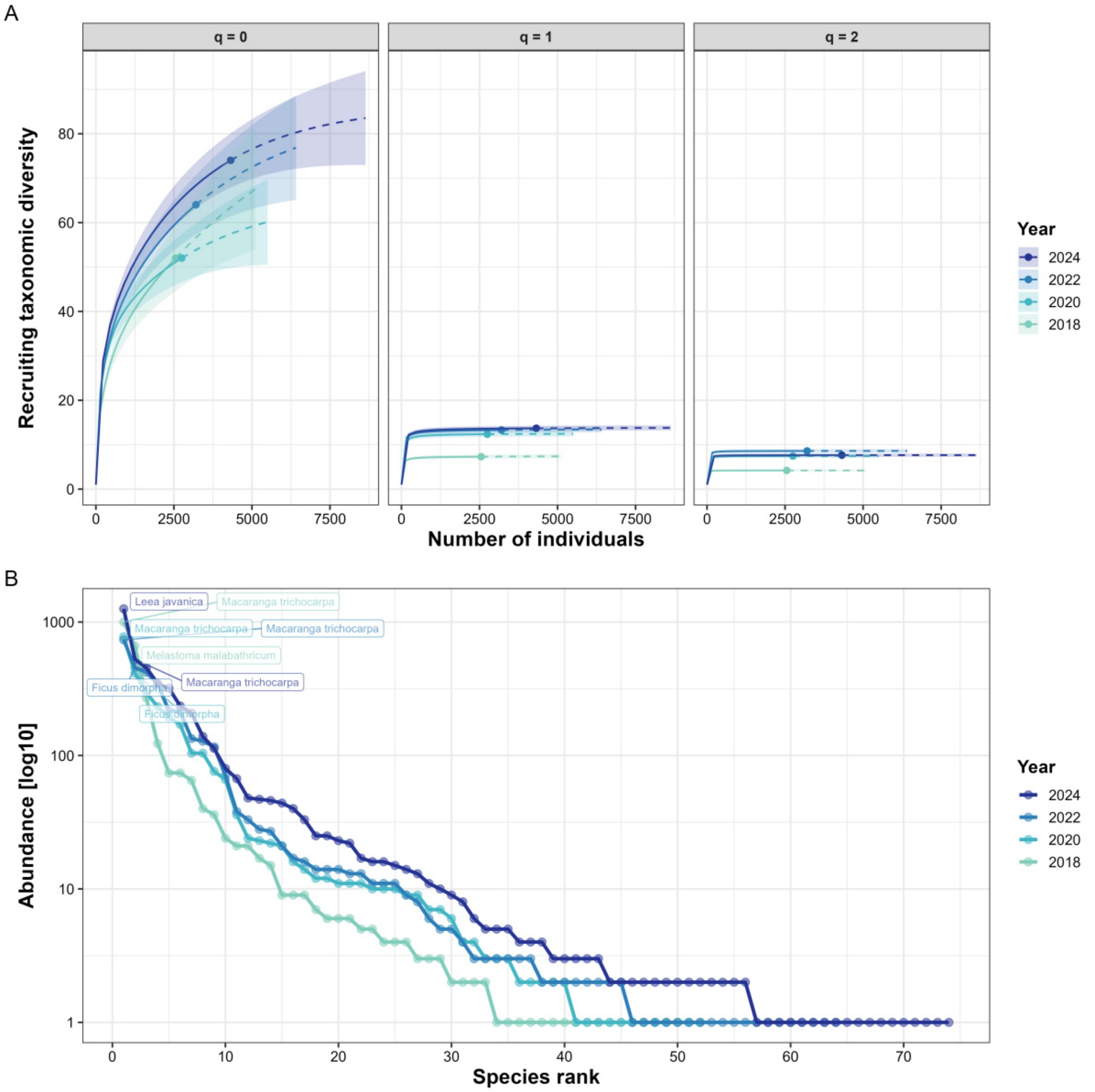

Figure 2: (A) Recruiting taxonomic diversity according to sample-size based rarefaction for four censused years (2018, 2020, 2022, 2024) and three q orders (0, 1, 2) at landscape scale. Solid lines represent rarefaction curves based on the complete censuses, solid points represent observed recruiting diversity, and dashed lines extrapolated values. Error bars represent 95% CIs from bootstrapping (N=500 randomizations). (B) Rank-abundance curves for four years (2018, 2020, 2022, 2024), with the two most abundant species per year labelled. Abundances are displayed in $\log_{10}$ scale.

For richness of very abundant species ($q = 2$), there was no further increase after 2022 ($TD_{2022} = 8.59$, $TD_{2024} = 7.64$; Figure 2A). The ten most abundant species remained the same over time and accounted for ~ 85 % of both individuals and basal area in 2024 (Figure S2). Nevertheless, dominant species ranks shifted strongly between years (Figure 2b, Figure S2). In 2018, there were two dominant species at landscape scale, *Macaranga trichocarpa* (Zoll.) Müll.Arg (Euphorbiaceae) and *Melastoma malabathricum* L. (Melastomataceae), while in 2024, *Leea javanica* Blume (Vitaceae) was the only dominant species, which showed a steep increase in both abundance and total basal area (Figure S2). In terms of total basal area, recruits of oil palm (*Elaeis guineensis* Jacq., Arecaceae) gained importance over the years (Figure S2).

Community evenness increased from 2018 to 2020, then slightly declined (Pielou's evenness $J'_{2018} = 0.50$, $J'_{2020} = 0.64$, $J'_{2022} = 0.62$, $J'_{2024} = 0.61$). The number of singletons (i.e. species represented by a single individual) ranged between 12 and 19 and showed no directional trend over time. Communities were sampled at 99 percent sampling coverage across all years and q orders (Figure S3).

The increase in recruiting diversity at landscape (gamma) scale was also reflected at the local (alpha) scale, with the average species richness per tree island increasing over time ($S_{2018} = 6.12 \pm 4.83$, $S_{2020} = 6.50 \pm 5.03$, $S_{2022} = 7.60 \pm 5.66$, $S_{2024} = 9.13 \pm 6.81$). However, time only explained little variation compared to the heterogeneity found between different tree islands within the same year (Permanova test: $p < 0.001$, $R^2 = 0.033$). Local evenness changed markedly over time, with some tree islands becoming more even as dominant species declined and more species were added, while other tree islands became more dominated by *Swietenia macrophylla* or *Leea javanica*. Yet, even in strongly dominated islands, local species richness continued to rise.

3.2.1 Trajectories of native, alien, and native forest-associated species

Landscape-scale native richness increased strongly from 2020 to 2024 (q = 0), but slowly saturated for q = 1 or declined slightly for q = 2 (Figure 3). In contrast, alien species diversity showed only a marginal increase for q = 0 and linearly decreased for q = 1 and q = 2, indicating that the overall rise in landscape-scale richness was driven primarily by native species. Alien abundance and total basal area increased linearly (Figure S4), as a few species accounted for a disproportionately high share of individuals. The average proportion of native species per tree island remained high (83-88%).

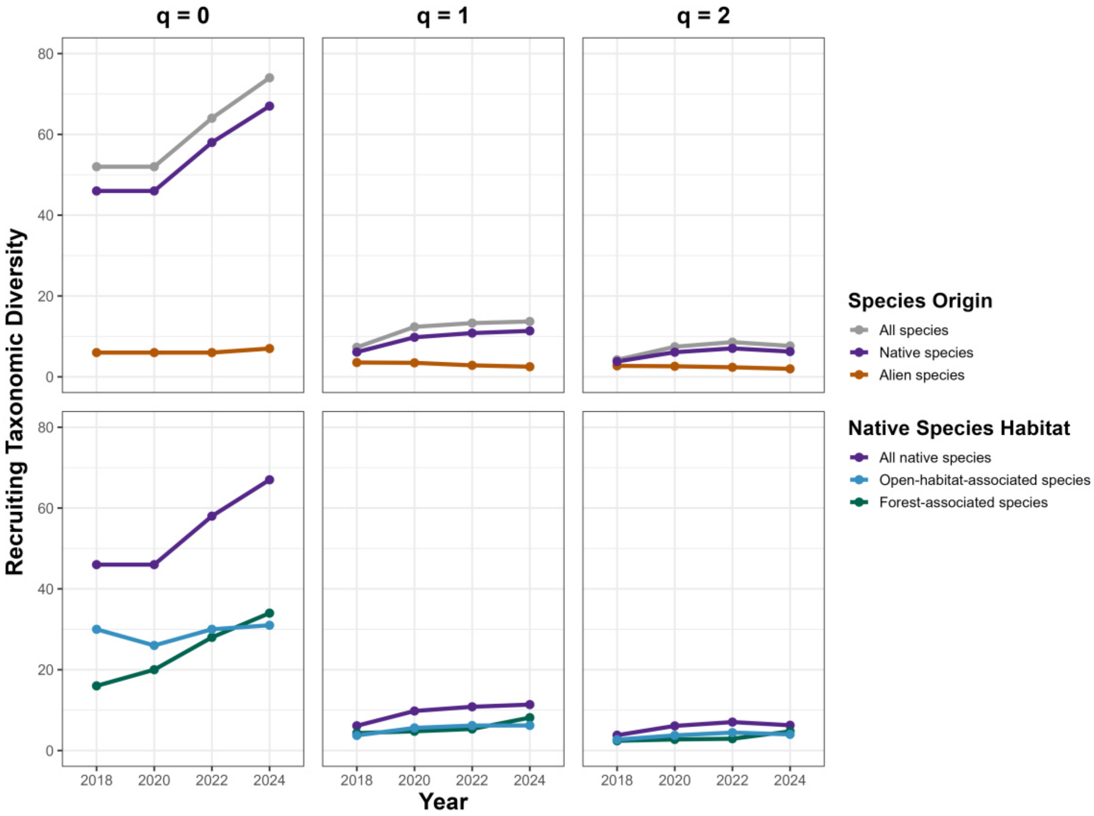

Figure 3: Recruiting taxonomic diversity of native versus alien species (top) and habitat types (bottom) of native species (open habitats, forest) over for four censused years (2018, 2020, 2022, 2024) at three q orders (0, 1, 2).

Native forest-associated recruiting diversity increased steadily for all q orders at landscape scale, eventually exceeding native open-habitat recruiting diversity (Figure 3). By 2024, 47 % of all species were native forest-associated species, compared to 31 % in 2018. Abundance and basal area remained higher for native open-habitat-associated species, while curves saturated for native forest-associated species (Figure S4). By 2024, native forest-associated species accounted for 20% of all individuals and 22% of total basal area.

3.3 Effects of tree island area and planted tree diversity over time

At the local (alpha) scale, year had a positive effect on recruiting diversity of native forest-associated species for $q = 0$ (std. $\text{beta}_{2024} = 0.46$, $p < .001$, 95% confidence interval (CI) [0.37, 0.56]; Figure 4; Table S2). Tree island area also increased local diversity, with effect sizes decreasing from $q = 0$ to $q = 2$ (std. beta = 0.45 [$q = 0$], 0.36 [$q = 1$], 0.32 [$q = 2$]; Table S2). No interaction between year and area was detected (Figure 4; Table 2). Planted tree diversity had a positive main effect on recruiting diversity for all q orders (std. $\text{beta}_{q0} = 0.15$, $p = 0.015$, 95% CI [0.03, 0.26]; Figure 4; Table S2). However, there was a significant negative interaction between year and planted tree diversity, indicating declining influence of planted tree diversity through time for all q orders (std. $\text{beta}_{2024,q0} = -0.15$, $p = 0.002$, 95% CI [-0.24, -0.05]; Figure 4; Table S2). Overall, the mixed-effects models accounted for most of the variance ($R^2_{q0} = 86\%$, $R^2_{q1} = 81\%$, $R^2_{q2} = 76\%$), with most explained by fixed effects ($R^2_{q0,\text{fixed}} = 57\%$, $R^2_{q1,\text{fixed}} = 49\%$, $R^2_{q2,\text{fixed}} = 42\%$). The proportion of variance explained declined with increasing q orders (Table S2). These results were also consistent when considering all native species (Figure 5; Table S3).

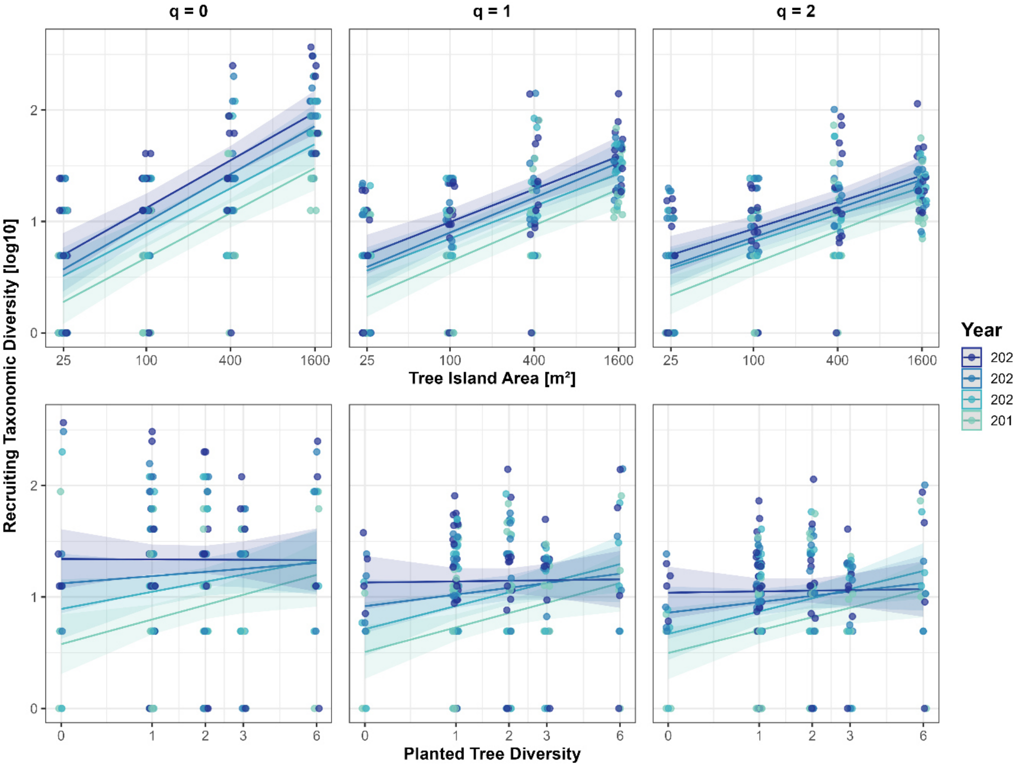

Figure 4: LMM predictions for tree island area (top) and planted tree diversity (bottom) effects on native forest-associated recruiting diversity (S = 35) at three q orders (0, 1, 2) for four censused years (2018, 2020, 2022, 2024). The response variable recruiting diversity is log10 transformed. The predictors tree island area and planted tree diversity are scaled and log10 transformed. The x-axis annotation shows actual values.

In contrast to native recruiting species, the local diversity of alien recruiting species did not increase with time (Figure 5; Figure S5; Table S4). Furthermore, tree island area was the only predictor that consistently increased local alien recruiting diversity across all q orders, while planted tree diversity showed a (non-significant) negative effect on alien recruiting diversity (Figure 5; Figure S5; Table S4).

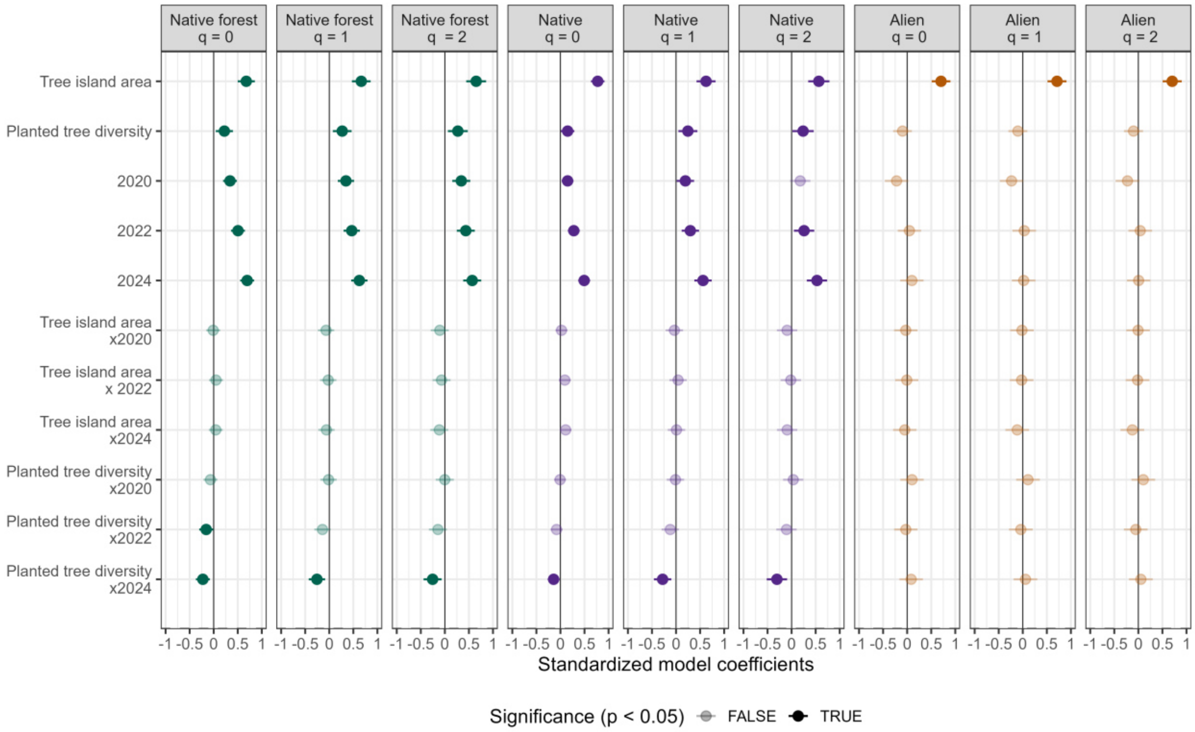

Figure 5: Standardized model coefficients for native forest-associated recruits (left), native recruits (center) and alien recruits (right) at three q orders (0, 1, 2). Transparent circles represent non-significant predictors (p > 0.05).

4 Discussion

It is well established that forest restoration through natural regeneration is an inherently long-term process (e.g. Gilman et al., 2016; Poorter et al., 2023, Brancalion et al., 2025). However, how much native woody diversity can be recovered within industrial-scale plantations through natural regeneration remains poorly understood (Song et al., 2025), and studies assessing how initial restoration approaches shape restoration pathways over longer time frames (> 5 years) are scarce (Holl et al., 2020; Paterno et al. 2024). The present findings show that the diversity and abundance of recruiting woody species within tree islands embedded in an industrial-scale oil palm plantation increased steadily over a decade of regeneration, with no signs of saturation. The consistently high proportion of native species, together with the progressive accumulation of native forest-associated taxa and the absence of evidence for alien-driven successional arrest, indicates that tree islands can facilitate the ecological recovery of native diversity at the landscape scale. At the local scale, initial restoration treatments were important predictors of native forest-associated recruiting diversity over time. Larger tree islands sustained a positive effect on native recruiting diversity while initial planted tree diversity enhanced native recruiting diversity at earlier stages but diminished over time.

4.1 Temporal changes in recruiting diversity and abundance

Recruiting diversity and abundance increased over time at landscape scale for both all (species richness, q = 0) and common species (q = 1) (Figure 2). This supports my hypothesis (H1) that cumulative dispersal events and increasing vegetation development progressively enrich communities. Considering the lack of forest patches in the surrounding landscape, the continued increase in landscape diversity suggests that long-distance seed dispersal by animals remains an important mechanism underlying this sustained increase (Poorter et al., 2023), as most recruiting species in the study system are animal-dispersed (Paterno et al., 2024). The persistence of a high number of singletons suggests ongoing arrivals of locally rare species and further increases in recruiting diversity.

The observed temporal increase in taxonomic diversity and abundance of recruiting species over time aligns with a forest restoration experiment in Costa Rica, where 54 tree species recruited during the first four years of the experiment, with > 90 % early-successional species, across natural regeneration and planted sites, and even in areas with minimal surrounding forest cover (Zahawi et al., 2013). In another Costa Rican wet-forest reforestation experiment, a substantial increase in taxonomic diversity was also reported over the first five years of natural regeneration (Gilman et al., 2016). However, the time required for forest restoration to achieve complete recovery relative to tropical old-growth forests remains difficult to predict (Brancalion et al., 2025). For instance, in a meta-analysis of secondary forest regrowth on abandoned agricultural land in the Neotropics, Rozendaal et al. (2019) found a median time of five decades for the recovery of species richness, and centuries for the full recovery of species composition.

Beyond the increase in taxonomic diversity, the gain of species, genera and families over time in the present study (Figure 1) also reflects an increase in phylogenetic diversity, particularly as more families were added each year. An increase in functional diversity over time can also be anticipated, since ecological strategies are partly conserved within plant families (Cornwell et al., 2014). While markedly higher taxonomic, phylogenetic and functional recruiting diversity was found in the tree island study system as compared to oil palm plantation (Paterno et al., 2024), a meta-analysis of tropical forest succession chronosequences moreover found an increase over time in functional diversity alongside with taxonomic diversity (Van der Sande et al., 2024). Because phylogenetically and functionally distinct species contribute disproportionately to ecosystem processes (Garbowski et al., 2025), enhancing phylogenetic and functional diversity in restoration at the landscape-scale is key to improving ecosystem functioning and trophic interactions, and fostering stable, resilient ecosystems (Ceulemans et al., 2019; De Bello et al., 2021; Wang et al., 2022; Garbowski et al., 2025).

At the local scale, however, I found strong variations in diversity, abundance, and species' dominances among tree islands, highlighting the stochasticity of local trajectories. This aligns with previous observations of significantly differing community assemblies and recovery rates of woody diversity among nearby restoration sites (e.g. Zahawi et al., 2013; Brancalion et al., 2025). Differences in local site conditions, biotic interactions, life-history traits and environmental stochastic variation likely contribute to divergent pathways (Poorter et al., 2023).

4.2 Recovery of native forest-associated species

Native forest-associated diversity increased steadily over time at landscape scale, simultaneously to a decline in native open-habitat associated diversity (Figure 3). This observed pattern is consistent with my hypothesis (H2) and can be explained by more favorable conditions for open-habitat-associated species at early successional stages and the development of more shaded conditions later in succession, favoring the establishment of native forest-associated species (Valladares et al., 2016; Poorter et al., 2023).

Alien species did not show a clear increase in diversity at landscape scale over time, and the diversity of common and abundant alien species was declining (Figure 3). This pattern supports the predicted earlier saturation of alien recruiting diversity, consistent with my hypothesis (H3). While rapid colonization and fast growth are common traits among alien species that allow them to succeed early in succession in productive environments (Gioria et al., 2023; Poorter et al., 2023), the underrepresentation of later successional alien species in the regional species pool (Gioria et al., 2023) likely explains the early saturation of alien diversity in this experiment.

In the present study, no clear evidence emerged for arrested succession under local dominance of alien species such as *Swietenia macrophylla*. Tree islands in which *Swietenia macrophylla* became dominant still accumulated additional species over time. Nonetheless, persistent dominance of alien species may lead to arrested succession in the future, reducing native diversity (cf. Matos et al., 2022). These findings highlight the importance of continued monitoring to identify emerging constraints on tree-island succession and the capacity of tree islands to provide habitats for native species.

4.3 Long-term effects of experimental treatments

Tree island area had a positive effect on recruiting diversity, including on native forest-associated species, though, this effect did not strengthen over time (Figure 4; Figure 5). The general finding of increased diversity in larger islands is consistent with the well-established species-area relationship (Arrhenius, O., 1921), explained by higher colonization probabilities combined with lower extinction risks for recruiting species in larger versus smaller islands (MacArthur and Wilson, 1967; Rosenzweig, M., 2003). Similar area effects on species richness were reported for tree islands by Zahawi and Augspurger (2006). In another tree island study, larger islands also contained higher densities of animal-dispersed recruits (Zahawi et al., 2013). The absence of interaction between time and tree island area does not support my hypothesis (H4) that time would further increase the positive effect of larger islands on recruiting diversity through the development of greater habitat heterogeneity. The absence of a positive feedback with time could reflect that habitat heterogeneity did increase substantially more in larger than in smaller islands during the transition from open to more shaded conditions. Another possible explanation is that greater habitat heterogeneity in larger islands facilitates a more diverse set of recruits but that this is counteracted by limited space and increased competition for establishment as vegetation develops over time. To my knowledge, the interaction between time and restoration area size has not yet been tested in comparable studies, highlighting the need for future work to determine whether larger restoration units eventually amplify their influence on successional dynamics.

Higher planted tree diversity initially promoted recruiting diversity, while its positive effect diminished over time (Figure 4; Figure 5). This interaction between planted tree diversity and time supports my hypothesis (H5) that higher planted diversity creates more heterogeneous conditions that facilitate the establishment of a wider set of recruits, and that over time the growth of recruiting species creates similar conditions in tree islands with low initial planted diversity or no planted trees, reducing the initial effect. The higher productivity of trees in more diverse plantings (Zemp et al., 2019; Jensen et al., 2025), the positive effect of neighborhood diversity on tree growth (Zheng et al., 2025), or the reduced variability in tree survival in mixed species plantings (Blondeel et al., 2024) might also have contributed to this initial effect. Enhanced productivity by planted trees may accelerate the establishment of more sensitive and shade-tolerant recruits by creating more dense vegetation and shaded conditions. In contrast, on alien recruiting diversity, planted tree diversity showed a sustained negative trend (Figure 5; Figure S5), which may support the proposed increased resistance of diverse plantings to possible invasions by alien species (Elton 1958; Naeem et al., 2000; Perkins et al., 2011; Halassy et al., 2023).

Interestingly, I found that the widely proposed strengthening of tree diversity effects on productivity and other ecosystem functions (e.g. Tatsumi, S., 2020; Chen et al., 2025; Zheng et al., 2024) was not sustained over time for natural regeneration of native diversity. While facilitation by diverse planted trees might be important during early succession (Paterno et al., 2024), niche competition may become more influential at later stages as vegetation density increases (Poorter et al., 2023). In line with these results, planted trees were found to facilitate natural recruitment also at other study sites; for example, recruitment of animal-dispersed tree species was found more than twofold higher in planted than non-planted areas (Zahawi et al., 2013). Contrastingly, Gilman et al. (2016) found no differences in recruiting diversity among planting treatments (0, 3, 6, 9, 12 planted species) over the first five years of succession. Here I demonstrated that initial restoration treatments varied in their influence over time, indicating that longer-term analyses of restoration outcomes are critical for understanding how early design choices shape successional trajectories and long-term biodiversity recovery.

4.4 Implications for restoration planning and monitoring

Overall, this study provides experimental evidence that tree islands, coupled with natural regeneration, represent a promising strategy to enhance native forest-associated woody diversity in ecologically impoverished oil palm landscapes. This further supports the idea that natural regeneration and tree islands are cost-efficient restoration strategies (Crouzeilles et al., 2020; Holl et al., 2020; Brancalion et al., 2025). Planting only six native tree species in relatively small areas within the oil palm matrix, led to the natural recruitment of 82 additional woody species over ten years, including 35 native forest-associated species. This finding provides strong evidence that even small, strategically established tree islands can catalyze substantial biodiversity recovery within heavily modified plantation landscapes.

Yet, even though an increasing number of native forest-associated species establishes in the tree islands over time, the predicted diversity of 83.5 woody species in the tree islands (Figure 2) is still far from the diversity levels found in lowland rainforest. Harapan Rainforest and Bukit Duabelas National Park, which can serve as reference forests in the study region, despite being classified as primary degraded forests (Margono et al., 2014), were reported to harbor more than 800 species of woody trees and shrubs, with alien species being almost completely absent (Rembold et al., 2017). Generally, recovering forests and especially agroforestry systems are known to fall short in biodiversity as compared to primary forests, with their communities often lacking later successional, dispersal-limited and rarer species, even after multiple decades of regeneration (Brancalion et al., 2025; Song et al., 2025). Therefore, while tree islands can substantially enhance biodiversity within plantation landscapes, they cannot substitute primary forests and must be considered as a complementary strategy to conserving large, intact forest areas which are essential for sustaining native forest-associated diversity (Norden et al., 2009; Rembold et al., 2017; Watson et al., 2018).

Beyond the positive effects of tree island area and planted tree diversity, biodiversity outcomes of tree islands could be further enhanced at landscape scale by actively reintroducing desired species, such as later-successional or dispersal-limited rare species (Cole et al., 2010; Holl et al., 2020; Holl et al., 2022; Joyce et al., 2025), controlling invasive species (e.g. Heleno et al., 2010; Weidlich et al., 2020; Halassy et al., 2023), and planting early-successional natives to preoccupy niches, limit invasive establishment, and prevent arrested succession (Halassy et al., 2023; Matos et al., 2022). Moreover, landscape-wide benefits of tree islands can be amplified by allowing their expansion into the surrounding oil palm matrix as per applied nucleation (e.g. Zahawi and Augspurger, 2006; Holl et al., 2020; Werden et al., 2022), which requires reduced conventional oil palm management in the zones surrounding tree islands and could serve as a pathway for regenerating secondary forests when oil palm cultivation is no longer profitable (Paterno et al., 2024).

With the loss of forest-dependent woody species in the oil palm landscape being accompanied by declines in animal diversity (Rembold et al., 2017), tree islands can be expected to provide increasingly valuable habitats to multiple animal taxa as they accumulate woody diversity and structural complexity over time (Kikuchi et al., 2024). For instance, a significant increase in bird diversity was observed 10 years after the onset of natural regeneration in the tree islands, with evidence that tree islands also attract birds to the wider landscape (Geske et al., 2025). Similarly, in a tree island study in Honduras, birds showed a strong preference for tree islands as compared to open pasture (Zahawi and Augspurger, 2006). In turn, birds are expected to enhance seed dispersal and recruitment of later-successional woody species in the tree islands, becoming increasingly important as succession progresses (Poorter et al., 2023). In the forest restoration experiment in Costa Rica (Zahawi et al., 2013; Holl et al., 2020), the number of animal-dispersed seeds increased significantly over the first nine years of natural regeneration. As trees begin fruiting, tree islands may also attract long-tailed macaques (*Macaca fascicularis*) that likely play a key role in long-distance seed dispersal in the study area (Paterno et al., 2024), being assessed as important dispersal agents especially in disturbed and fragmented habitats (Albert et al., 2014; Corlett R. T., 2017). Continued long-term monitoring of both woody diversity and the temporal effects of tree islands on other taxa and biodiversity dimensions will be crucial to address current knowledge gaps (Brancalion et al., 2025) and to evaluate restoration strategies in industrial-scale plantation landscapes more comprehensively.

5 Conclusions

This study demonstrated a pronounced, decade-long increase in woody diversity within tree islands undergoing natural regeneration. It was shown that the initial restoration design strongly governs regeneration pathways, with larger tree islands and higher planted tree diversity enhancing starting conditions for natural regeneration. Yet, despite the continued arrival of native forest-associated species, tree islands had recovered only a small fraction of the total woody diversity present in primary reference forests. As tree islands are transitioning from open-habitat-associated towards more forest-associated assemblages, the existence of primary forests as main reservoirs of native forest-associated diversity, in combination with long-distance seed dispersal by animals, will be increasingly critical for sustaining succession over time. Overall, this study demonstrated that tree islands can catalyze substantial recovery of native diversity within heavily modified plantation landscapes, while longer-term analyses of restoration outcomes are critical for understanding how early design choices shape successional trajectories and long-term biodiversity recovery.

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8 Supplementary materials

Supplementary text

Local trajectories of dominant species

Community evenness varied locally. E.g. in 2024, relative abundances of the locally most abundant species ranged from 17 % to 91 % (*Ficus dimorpha*) between tree islands. Over time, local dominance of *Macaranga trichocarpa* and *Ficus dimorpha* decreased*,* as communities recruited more individuals and became more even locally (e.g. decline from 89 % (2018) to 45 % (2024); *Macaranga trichocarpa*, island 51, or from 80 % (2018) to 45 % (2024); *Macaranga trichocarpa*, island 47). In contrast, other tree islands became more dominated over time, especially by *Swietenia macrophylla* or *Leea javanica* (e.g. increase from 0 % (2018) to 76 % (2020) up to 80 % (2024, out of 234 individuals); *Swietenia macrophylla,* island 30, or from 0 % (2018 – 2022) to 81 % (2024), *Swietenia macrophylla,* island 15). For *Leea javanica*, there was an increasing trend in relative abundance for the 28 tree islands where the species occurred - most significant increase in island 7 from 4 % (2018) to 61 % out of 638 individuals in 2024. Interestingly, despite the increasing dominance of single species such as *Swietenia macrophylla* and *Leea javanica* in the previously mentioned tree islands, still a trend towards greater local species richness occurred across these islands over time ($S_{2018\text{-}2024(\text{island } 30)} = [3,9,9,10]$; $S_{2018\text{-}2024(\text{island } 15)} = [4,3,8,9]$; $S_{2018\text{-}2024(\text{island } 07)} = [12,12,15,18]$).

Supplementary figures

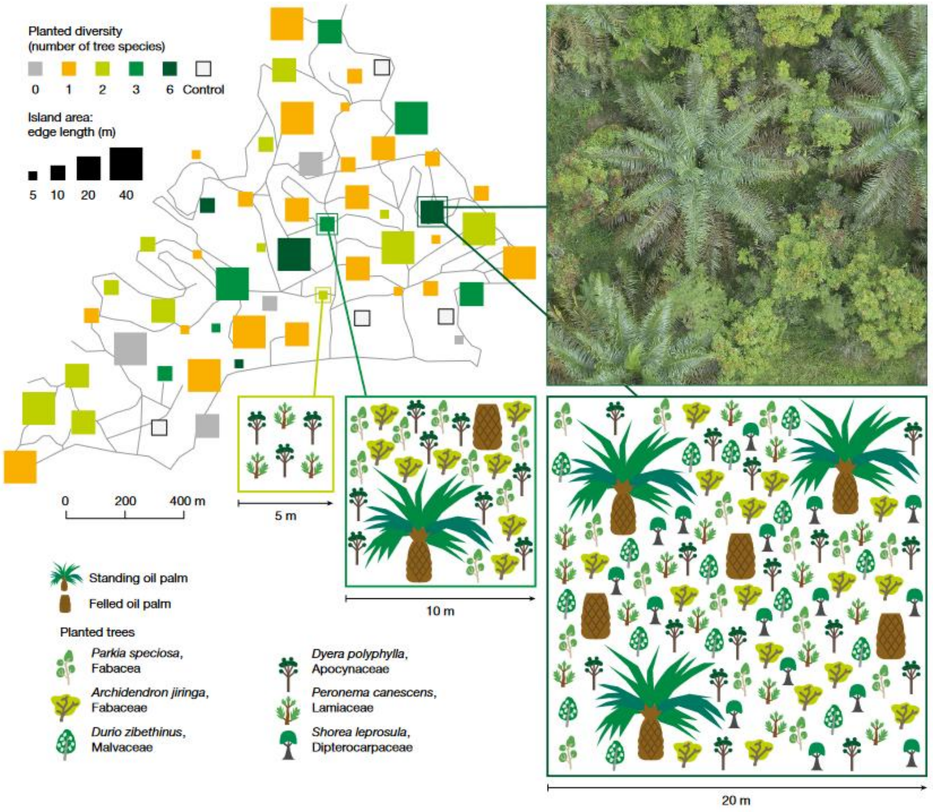

Figure S1: Zemp et al., 2023. Experimental design of the EFForTS-BEE sites: (i) Distribution of tree islands across the industrial oil palm plantation (top left). Tree islands are represented as squares of four sizes (representing tree island areas) and six colors (representing planted tree diversity levels), including controls, following a random partitions design. (ii) Aerial photograph of a tree island (top right). (iii) Tree island design consisting of oil palms (9 m -grid) and planted trees (2 m -grid) (bottom). For more details, please refer to Teuscher et al., 2016.

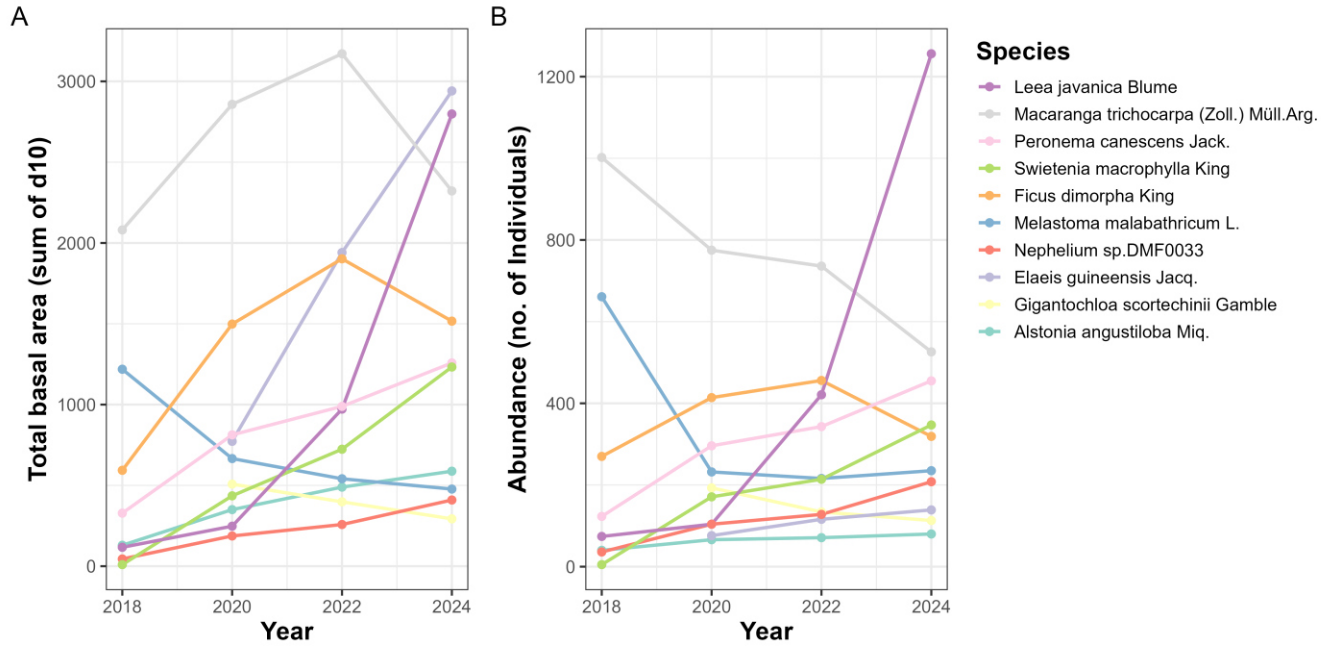

Figure S2: Trajectories (2018-2024) of total basal areas (A) and abundances (B) of the ten most abundant species in 2024, together accounting for ca. 85% of both abundance and basal areas in 2024. Total basal area is calculated as the sum of d10 (stem diameter at 10 cm) of all main stems. The legend displays species in decreasing order based on 2024 abundance.

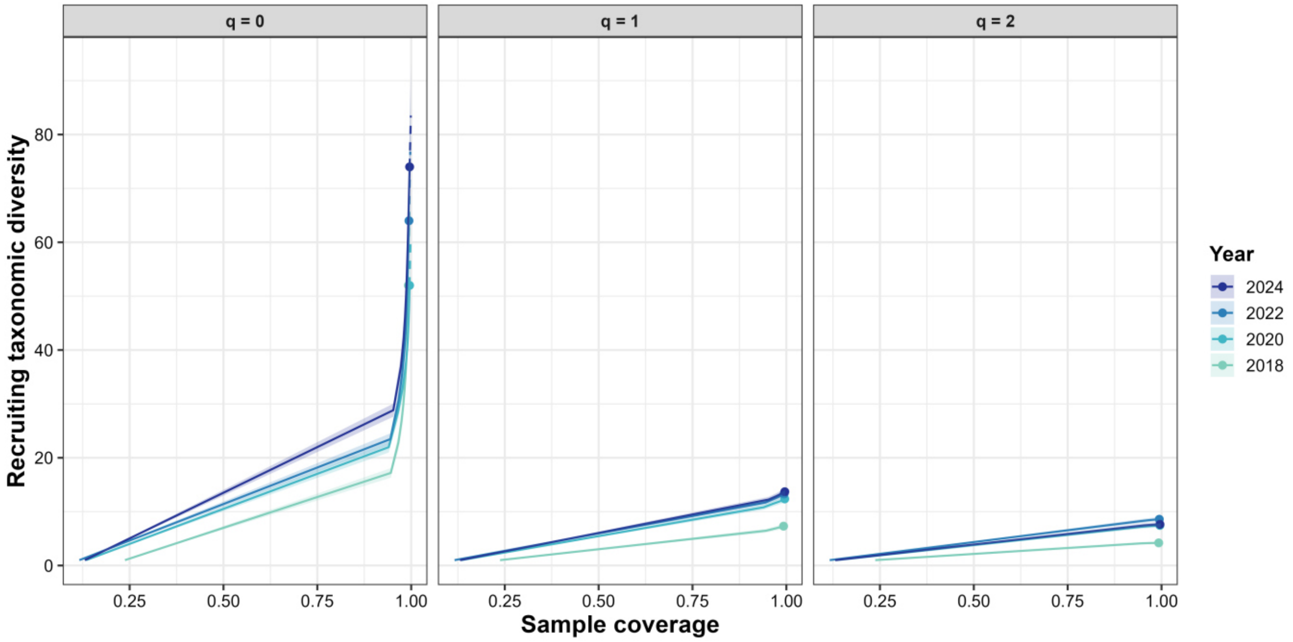

Figure S3: Recruiting taxonomic diversity according to coverage-based rarefaction for four censused years (2018, 2020, 2022, 2024) and three q orders (0, 1, 2) at landscape scale. Solid lines represent rarefaction curves based on the complete censuses, solid points represent observed recruiting diversity, and dashed lines extrapolated values.

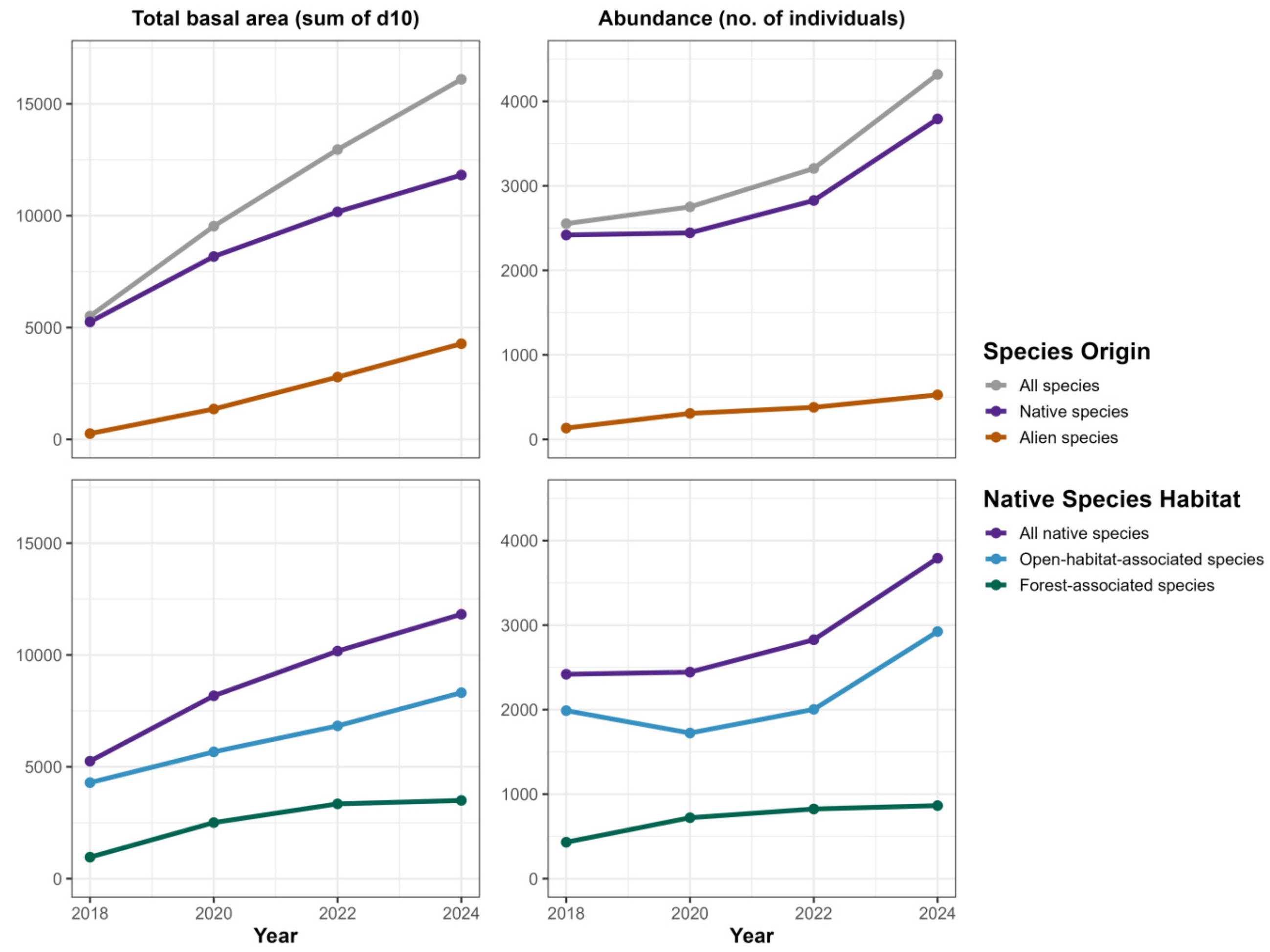

Figure S4: Recruiting total basal area (left) and abundance (right) of native versus alien species (top) and habitat types (bottom) of native species (open habitats, forest) for four censused years (2018, 2020, 2022, 2024). Total basal area is calculated as the sum of d10 (stem diameter at 10 cm) of all main stems.

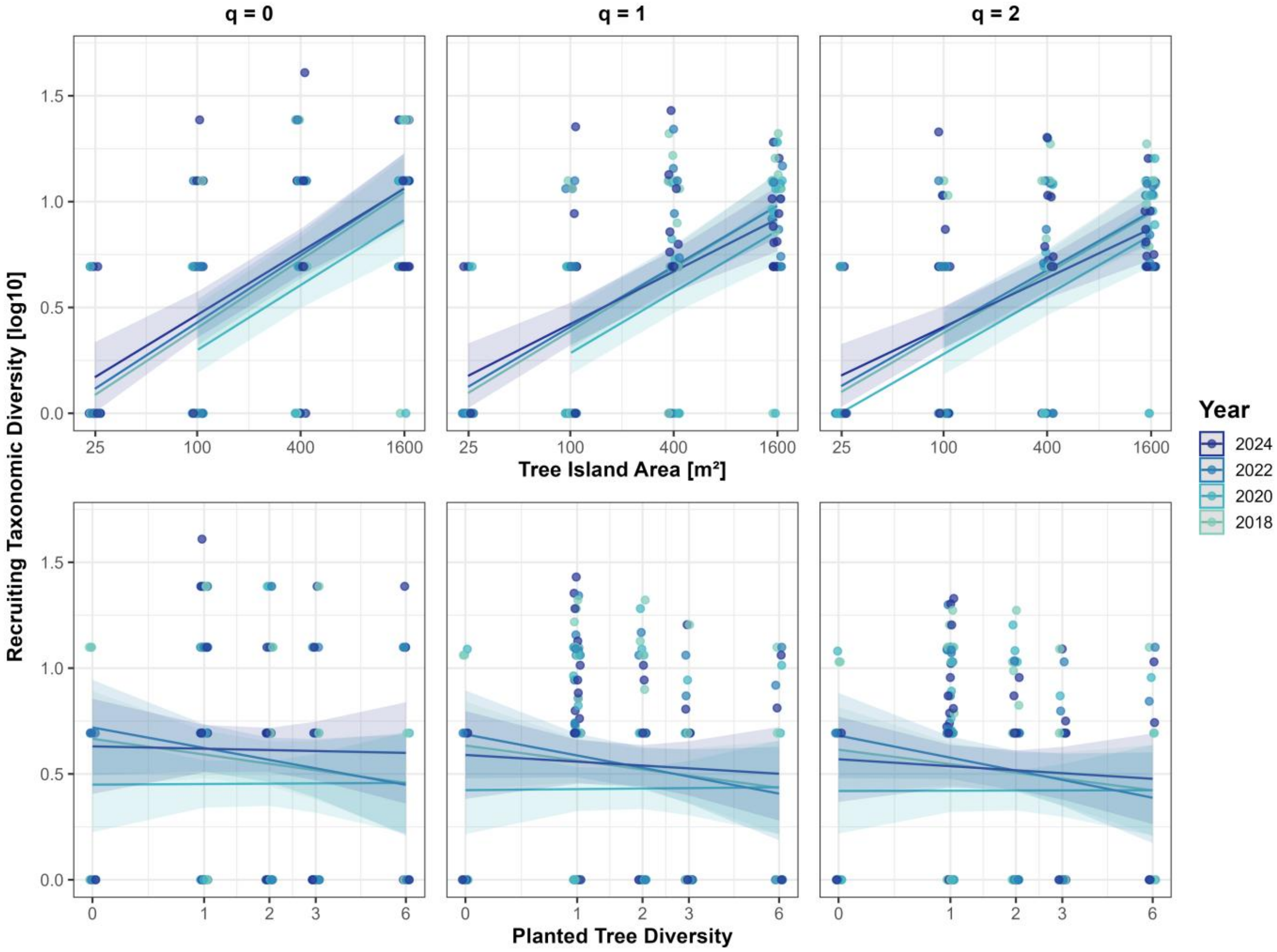

Figure S5: LMM predictions for tree island area (top) and planted tree diversity (bottom) effects on alien recruiting diversity (S = 8) at three q orders (0, 1, 2) for four censused years (2018, 2020, 2022, 2024). The response variable recruiting diversity is log10 transformed. The predictors tree island area and planted tree diversity are scaled and log10 transformed. The x-axis annotation shows actual values.

Supplementary tables

Table S1: List of recruiting liana species in 2024, with respective lifeform, origin, habitat, 2024 abundance and tree island occupancy (i.e. percentage of tree islands in which the species is present). Families and respective species are listed in alphabetical order.

Family	Species	Lifeform	Origin	Habitat	2024	Occupancy 2024 (%)
Annonaceae	*Uvaria cf. grandiflora* Roxb. ex Hornem.	liana	native	forest	1	1.92
Apocynaceae	*Chonemorpha verrucosa* (Blume) D.J.Middleton	liana	native	forest	22	5.77
Apocynaceae	*Secamone sp.KR5266*	liana	native	NA	50	21.15
Celastraceae	*Reissantia cassinoides* (DC.) Ding Hou	liana	native	forest	7	9.62
Combretaceae	*Combretum cf. sundaicum* Miq.	liana	native	open	63	25.00
Convolvulaceae	*Bonamia semidigyna* (Roxb.) Hallier f.	liana	native	open	9	3.85
Convolvulaceae	*Camonea pilosa* (Houtt.) A.R.Simões & Staples	liana	native	open	90	15.38
Convolvulaceae	*Erycibe rheedei* Blume	liana	native	open	2	3.85
Dilleniaceae	*Tetracera scandens* (L.) Merr.	liana	native	open	2	1.92
Fabaceae	*Calopogonium mucunoides* Desv.	liana	alien	open	3	1.92
Fabaceae	*Centrosema molle* Mart. ex Benth.	liana	alien	open	8	11.54
Fabaceae	*Derris amoena* Benth.	liana	native	open	7	1.92
Fabaceae	*Mezoneuron sumatranum* (Roxb.) Wight & Arn. ex Voigt	liana	native	open	1	1.92
Fabaceae	*Millettia sericea* (Vent.) Wight & Arn. ex Hassk.	liana	native	open	2	1.92
Fabaceae	*Mucuna biplicata* Teijsm. & Binn. ex Kurz	liana	native	open	26	21.15
Fabaceae	*Phanera semibifida* (Roxb.) Benth.	liana	native	open	36	25.00
Gnetaceae	*Gnetum tenuifolium* Ridl.	liana	native	forest	2	3.85
Melastomataceae	*Macrolenes cf. dimorpha* (Craib) J.F.Maxwell	liana	native	open	3	1.92
Menispermaceae	*Arcangelisia flava* (L.) Merr.	liana	native	forest	1	1.92
Oleaceae	*Jasminum elongatum* (P.J.Bergius) Willd.	liana	native	open	1	1.92
Phyllanthaceae	*Bridelia cinnamomea* Hook.f.	liana	native	forest	3	1.92
Primulaceae	*Maesa sumatrana* Scheff.	liana	native	open	4	3.85
Resedaceae	*Stixis scortechinii* (King) M.Jacobs	liana	native	open	5	5.77
Rubiaceae	*Coptosapelta cf. tomentosa* (Blume) Valeton ex K.Heyne	liana	native	forest	6	1.92

Rubiaceae	*Mussaenda frondosa* L.	liana	native	open	4	5.77
Rubiaceae	*Uncaria attenuata* Korth.	liana	native	open	24	21.15
Rubiaceae	*Uncaria cordata* (Lour.) Merr.	liana	native	open	17	23.08
Vitaceae	*Tetrastigma coriaceum* (DC.) Gagnep.	liana	native	open	9	5.77

Table S2: LMM outputs for native forest-associated recruiting diversity at 3 q orders (0, 1, 2).

	q=0			*q=1*			*q=2*		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Intercept	0.88	0.76 – 0.99	**<0.001**	0.80	0.70 – 0.91	**<0.001**	0.77	0.67 – 0.87	**<0.001**
Tree island area	0.45	0.33 – 0.57	**<0.001**	0.36	0.25 – 0.47	**<0.001**	0.32	0.22 – 0.43	**<0.001**
Planted tree diversity	0.15	0.03 – 0.26	**0.015**	0.15	0.04 – 0.25	**0.007**	0.13	0.03 – 0.24	**0.011**
2020	0.22	0.13 – 0.32	**<0.001**	0.19	0.10 – 0.28	**<0.001**	0.17	0.08 – 0.26	**<0.001**
2022	0.33	0.24 – 0.43	**<0.001**	0.25	0.16 – 0.35	**<0.001**	0.22	0.12 – 0.31	**<0.001**
2024	0.46	0.37 – 0.56	**<0.001**	0.34	0.25 – 0.43	**<0.001**	0.28	0.19 – 0.38	**<0.001**
Tree island area x 2020	-0.01	-0.10 – 0.09	0.885	-0.04	-0.13 – 0.06	0.440	-0.05	-0.15 – 0.04	0.269
Tree island area x 2022	0.03	-0.06 – 0.13	0.514	-0.01	-0.10 – 0.08	0.799	-0.03	-0.13 – 0.06	0.466
Tree island area x 2024	0.03	-0.07 – 0.12	0.560	-0.03	-0.12 – 0.06	0.493	-0.06	-0.15 – 0.04	0.226
Planted tree diversity x 2020	-0.04	-0.14 – 0.05	0.360	-0.01	-0.10 – 0.08	0.860	-0.00	-0.09 – 0.09	0.986
Planted tree diversity x 2022	-0.10	-0.20 – -0.01	**0.034**	-0.08	-0.17 – 0.02	0.101	-0.07	-0.16 – 0.02	0.133
Planted tree diversity x 2024	-0.15	-0.24 – -0.05	**0.002**	-0.14	-0.23 – -0.05	**0.003**	-0.13	-0.22 – -0.03	**0.008**
Random Effects									
σ^2	0.06			0.06			0.06		
τ_{00}	$0.13_{\text{plot\_id}}$			$0.09_{\text{plot\_id}}$			$0.08_{\text{plot\_id}}$		
ICC	0.67			0.62			0.59		
N	$52_{\text{plot\_id}}$			$52_{\text{plot\_id}}$			$52_{\text{plot\_id}}$		
Observations	208			208			208		
Marginal R^2 / Conditional R^2	0.573 / 0.859			0.487 / 0.805			0.422 / 0.763		

Table S3: LMM outputs for native recruiting diversity at 3 q orders (0, 1, 2).

	q=0			*q=1*			*q=2*		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Intercept	1.56	1.46 – 1.67	**<0.001**	1.22	1.12 – 1.32	**<0.001**	1.09	0.99 – 1.19	**<0.001**
Tree island area	0.59	0.48 – 0.69	**<0.001**	0.33	0.22 – 0.43	**<0.001**	0.26	0.16 – 0.36	**<0.001**
Planted tree diversity	0.11	0.01 – 0.22	**0.036**	0.13	0.03 – 0.23	**0.015**	0.11	0.01 – 0.21	**0.034**
2020	0.11	0.02 – 0.21	**0.018**	0.10	0.01 – 0.20	**0.035**	0.08	-0.01 – 0.18	0.096
2022	0.21	0.12 – 0.30	**<0.001**	0.16	0.06 – 0.25	**0.001**	0.12	0.02 – 0.22	**0.016**
2024	0.37	0.28 – 0.47	**<0.001**	0.30	0.20 – 0.39	**<0.001**	0.24	0.15 – 0.34	**<0.001**
Tree island area x 2020	0.02	-0.08 – 0.11	0.731	-0.02	-0.11 – 0.08	0.713	-0.04	-0.14 – 0.05	0.385
Tree island area x 2022	0.07	-0.02 – 0.16	0.145	0.02	-0.07 – 0.12	0.641	-0.01	-0.11 – 0.09	0.871
Tree island area x 2024	0.08	-0.01 – 0.18	0.086	0.01	-0.09 – 0.10	0.918	-0.04	-0.14 – 0.05	0.391
Planted tree diversity x 2020	-0.01	-0.10 – 0.09	0.900	-0.01	-0.10 – 0.09	0.900	0.02	-0.08 – 0.11	0.747
Planted tree diversity x 2022	-0.06	-0.15 – 0.03	0.200	-0.06	-0.16 – 0.03	0.192	-0.05	-0.15 – 0.05	0.325
Planted tree diversity x 2024	-0.11	-0.20 – -0.01	**0.025**	-0.15	-0.24 – -0.05	**0.003**	-0.14	-0.24 – -0.04	**0.005**
Random Effects									
σ^2	0.06			0.06			0.06		
τ_{00}	$0.09_{\text{plot\_id}}$			$0.09_{\text{plot\_id}}$			$0.07_{\text{plot\_id}}$		
ICC	0.61			0.58			0.54		
N	$52_{\text{plot\_id}}$			$52_{\text{plot\_id}}$			$52_{\text{plot\_id}}$		
Observations	208			208			208		
Marginal R^2 / Conditional R^2	0.736 / 0.898			0.472 / 0.779			0.342 / 0.698		

Table S4: LMM outputs for alien forest-associated recruiting diversity at 3 q orders (0, 1, 2).

	q=0			*q=1*			*q=2*		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Intercept	0.57	0.47 – 0.66	**<0.001**	0.54	0.45 – 0.63	**<0.001**	0.52	0.43 – 0.61	**<0.001**
Tree island area	0.36	0.26 – 0.46	**<0.001**	0.33	0.24 – 0.42	**<0.001**	0.31	0.23 – 0.40	**<0.001**
Planted tree diversity	-0.05	-0.15 – 0.05	0.330	-0.05	-0.14 – 0.04	0.312	-0.05	-0.13 – 0.04	0.317
2020	-0.11	-0.24 – 0.01	0.075	-0.11	-0.22 – 0.01	0.063	-0.10	-0.21 – 0.01	0.072
2022	0.02	-0.10 – 0.15	0.710	0.01	-0.10 – 0.13	0.806	0.02	-0.09 – 0.13	0.751
2024	0.05	-0.07 – 0.17	0.429	0.01	-0.10 – 0.12	0.878	0.00	-0.11 – 0.11	0.960
Tree island area x 2020	-0.02	-0.14 – 0.11	0.808	-0.01	-0.12 – 0.11	0.892	-0.00	-0.11 – 0.11	0.965
Tree island area x 2022	-0.00	-0.13 – 0.12	0.944	-0.01	-0.13 – 0.10	0.849	-0.01	-0.12 – 0.10	0.895
Tree island area x 2024	-0.03	-0.15 – 0.10	0.686	-0.05	-0.17 – 0.06	0.356	-0.06	-0.17 – 0.05	0.320
Planted tree diversity x 2020	0.05	-0.07 – 0.17	0.417	0.05	-0.06 – 0.16	0.386	0.05	-0.06 – 0.16	0.412
Planted tree diversity x 2022	-0.01	-0.14 – 0.11	0.815	-0.02	-0.13 – 0.10	0.746	-0.02	-0.13 – 0.09	0.670
Planted tree diversity x 2024	0.04	-0.08 – 0.17	0.505	0.03	-0.09 – 0.14	0.652	0.02	-0.09 – 0.13	0.676
Random Effects									
σ^2	0.10			0.09			0.08		
τ_{00}	$0.03_{\text{plot\_id}}$			$0.03_{\text{plot\_id}}$			$0.02_{\text{plot\_id}}$		
ICC	0.22			0.22			0.23		
N	$52_{\text{plot\_id}}$			$52_{\text{plot\_id}}$			$52_{\text{plot\_id}}$		
Observations	208			208			208		
Marginal R^2 / Conditional R^2	0.487 / 0.602			0.475 / 0.592			0.468 / 0.589		

Appendix 1: Field protocol

Note: The content of this protocol has been modified from the following resources:

- Paterno, G. et al., 2022. Tree inventory and plant functional traits. Detailed protocol for field sampling.
- Chave, J.,2006. Measuring wood density for tropical forest trees. A field manual.

Content:

1. **Experimental design (EFForTS-BEE)**
2. **Tree inventory**
3. **Specimen and sample collection**

1. Experimental design (EFForTS-BEE)

EFForTS-BEE is a tree diversity experiment within a large-scale oil-palm monoculture plantation in Jambi Province, Sumatra - Indonesia. The experiment consists of 52 tree islands that were planted within oil-palm plantations varying in size (5x5m, 10x10m, 20x20m and 40x40m) and diversity of tree species (0, 1, 2, 3, and 6). The six different multi-purpose tree species planted are shown in Table 1. In total, 6354 trees were planted in the experiment, while all species were equally represented across plots and treatments. Natural regeneration was allowed in all tree islands regardless of the diversity of planted trees. In addition to the tree islands, four control plots (10x10m) with management as usual oil-palm monoculture plantations were implemented. In total, EFForTS-BEE has 56 experimental plots (Fig. 1). All plots were fenced to avoid damage from large herbivores and human interference.

Table 1. Name, family, local use and local name of the six planted species in the EFForTS-BEE experiment.

Code	**Species**	**Family**	**Local use**	**Local name**
A	Parkia speciosa	Fabaceae	Fruit tree	Petai
B	Archidendron jiringa	Fabaceae	Fruit tree	Jengkol
C	Durio zibethinus	Malvaceae	Fruit tree	Durian
D	Dyera polyphylla	Apocynaceae	Natural latex and timber tree	Jelutung
E	Peronema canescens	Lamiaceae	Timber tree	Sungkai
F	Shorea leprosula	Dipterocarpaceae	Timber tree	Meranti

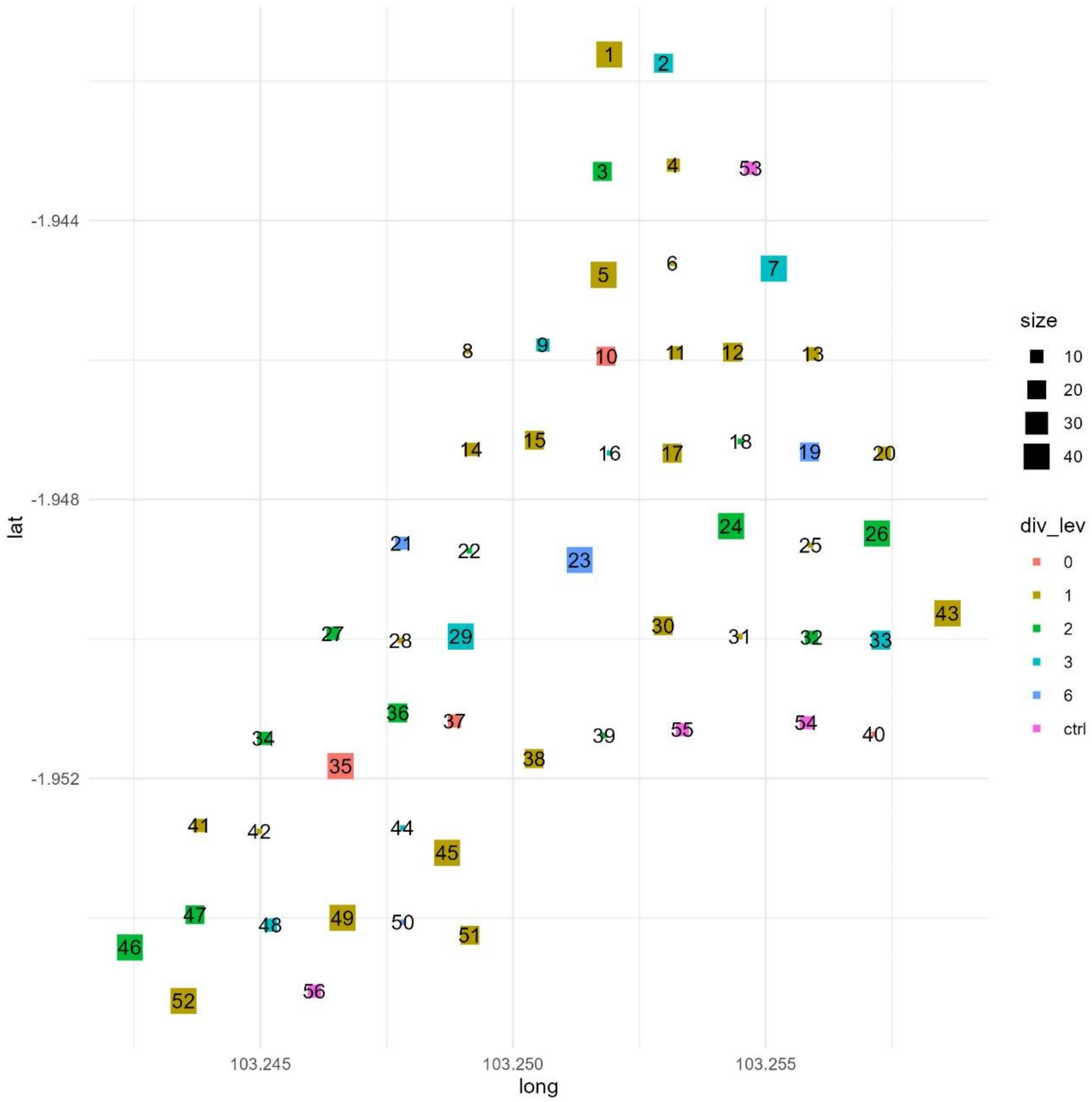

Figure 1. Experimental design and spatial distribution of tree islands and control plots from the EFForTS-BEE experiment. The 56 plots were randomly distributed across the oil palm plantation.

Standardized 5x5m subplots were established within each plot. Subplots were allocated at random within plots larger than 5x5m. Subplots were randomized considering a buffer zone of 1.5m from the plot edge. A table of all plot and subplot coordinates is given in appendix 1, helping to find the subplots in the field.

2. Tree inventory

Equipment

- Diameter measurement tape
- 10m measuring tape
- Disto and Clinometer
- Vertex IV box
- Compass
- Parang + knife
- Red spray paint + stencil
- Tree tags and rope
- Spare batteries
- GPS device
- 1.3m stick
- Plant identification literature
- Data from previous census
- Map of all plots

Workflow

The inventory starts at one corner of the plot, walking through the plot systematically along a zig-zag line. All free-standing woody plants (trees, shrubs, bamboos) inside the plot with a minimum height of 130 cm, hereafter referred to as “trees”, are recorded with all their stems.

1. Reaching minimum height?

The minimum height is tested with a 1.3-m-long stick. Only individuals showing a height of ≥ 1.3 m are included with all their stems in the inventory. Exceptions are previously recorded and tagged individuals that do not reach 130 cm height anymore due to stem breaks. These individuals are still censused.

In case of leaning trunks, the 1.3 m vertical height above the trunk center at soil level counts.

In case of recruited oil palms, only individuals with a minimum stem height of 10 cm combined with their total height of ≥ 1.3 m are included in the inventory.

2. Stems

All stems of an individual tree are tagged and measured individually. A stem is defined as a branching below 130 cm height that is contributing to or growing towards the main crown.

3. Alive or dead tree or stem?

Standing dead trees and stems are measured similarly to living trees, but a note is added that they are dead.

4. New individual or already censused?

3.1) New individual or stem

If the tree or stem does not have a tag and cannot be matched to any recorded individuals, it is a new individual.

a) Mark with a plastic number tag on the trunk (for each stem)
b) Measure tree position (distance and angle to nearest planted tree or oil palm)
c) Measure diameter (d10, dbh) (for each stem)
d) Measure inclination if the tree is not vertical (≥ 20° leaning) (for each stem)
e) Check for any stem breaks (for each stem)
f) Measure height
g) If necessary for species identification, remove a small (!) piece of bark to check for slash, sap.
h) Give the tree a preliminary species name ("field name")
i) Enter all data into the KOBO App (see codes below)

a) Tagging

- Choose a 5-digit tree tag number. Make sure that your number is the same as the one entered in the KOBO-App!
- If a tree has more than one stem, add one tag to each stem and note in the KOBO App that the tag-number of the second (and third, etc.) tag belongs to the first one. Start the thickest stem, followed by the 2nd thickest etc.

  In case of bamboos, select 3 stems for tagging (one small, one medium-sized, and one large stem) and note down the total number of stems.

b) Tree position (Disto and compass)

- Using the Disto, find the distance of the target tree to the nearest planted tree (tree ID 100 to 6453) or oil palm. Note the number of that nearest tree or oil palm.
- To get the two-dimensional position of the target tree in relation to the nearest planted tree or oil palm, use the compass pointing from the imagined centre of the tree to the nearest planted tree or oil palm and read the angle in degrees (°).

c) Diameter (Diameter tape)

- Diameter is measured at two heights:

  d10: the base of the stem (at 10 cm height)
  dbh: at breast height (1.3 m)
- To find the point of measurement, always measure from the starting point of the stem (don't include any roots!) 10 cm and 1.3 m along the length of the stem (= no vertical height). In case of manyfold branched stems, measure 10 cm and 1.3 m along the stem branches that are building the main crown of the stem.
- Exceptions:

  If there is a stem anomaly, or a branching at 1.3 m or the tree has buttresses or stilt roots, measure 10 cm above stem anomalies. In case of doubt, refer to Appendix 2. If d10 or dbh are not measured at 10 cm and 1.3 m, note down the respective point of measurement.
- Carefully remove lianas and epiphytes (if necessary, do not cut them!).
- Place the stencil (another diameter tape) to mark the position of dbh measurement and spray the red paint.
- Make sure to place the diameter tape exactly perpendicular to the trunk, measure the diameter and enter into the KOBO app (in cm with one decimal, e.g. 15.3 cm).
- If a tree has more than one stem, measure d10 and dbh for each stem.

d) Inclination (Clino or Vertex)

- If the tree is not vertical (≥ 20° leaning), note the inclination in degrees. The Clino measures angles from a horizontal line. A perfectly vertical tree would have a value of 90°, any value between 71° and 109° means that the tree is not leaning ≥ 20°.
- Place the device with the narrow side against the trunk at soil level and point the laser towards the crown tip.
- Press the angle button on the Disto. Read the angle in degrees.
- If the angle is ≤70° or ≥110°, enter the value. If the angle is between 71° and 109°, nothing needs to be entered.
- If a tree has more than one stem, measure inclination for each stem if needed.

e) Stem breaks and other observations

- Note if
  - the trunk or crown of a tree is severely broken or damaged above 1.3 m
  - stems show signs of an old break below 1.3 m
  - stems are leaning by more than 45°
- Note any other observation, e.g.
  - stem broken

- stem resprouting
- stem fluted and/or fenestrated
- hollow stem
- multiple stems
- burnt stem
- has lianas, >50% canopy covered by lianas
- evidence of disease
- standing dead tree
- anthropogenic removal, cut tree

f) Tree height (Pole or Vertex)

- Use the pole for smaller trees and the Vertex for taller ones (> 8 m).
- Measure vertical height of the tree always from soil level.
- The Vertex calculates height based on the trigonometric functions based on two angles and the distance. The measurement is a two-step process, measuring first the distance to the tree, then, the angle to the tree crown.
- Calibration: Turn on the transponder (the Vertex has to be off). Hold the transponder with the white side in front of the vertex front (vertex has to be turned off) and press the DME-button on the Vertex until the transponder makes two beeping sounds. Calibrate the device by using the 10m measuring tape, and repeat calibration at noon when the temperature changed more than 5-10°C.
- Distance: The person close to the tree places the transponder on the tree always at 1.3 m height facing the person with the Vertex. The other person holds the Vertex vertically in front of their face looking through the hole. Press ON aiming at the transponder until it beeps, and the hair cross sign starts blinking. The distance is now measured. Make sure to stand with the Vertex at least as many meters away from the tree as the tree's height.
- Angle: Now, aim the Vertex at the top of the tree and press again making the height measurement. You will hear another beep indicating that the height is now locked on the display. You can take up to 6 height measurements in case you aimed wrong. Make sure you don't change your position when doing the height measurement.
- Tree inclination: Make sure the tree is not inclined towards you or away from you, but you are in parallel to the inclination. Otherwise you over- or underestimate its height. On sloping terrain, try to measure parallel to the slope or from a position higher than the tree.
- Special cases:

  For particularly high and not clearly visible trees, at least three measurements from different positions are taken and the mean value used.
  Palm height is defined as the length from the base of the trunk to the base of the youngest leaf where we expect the meristem.

Standing dead trees with still firm wood (not completely rotten) can also be measured.

- IMPORTANT: The Vertex will give you a height measurement even if the transponder is off, or it cannot get its signal, as the default distance to the transponder is set at 20m. So be careful when the values of height are not what you would be expecting from the tree. Repeat the measurements if in doubt.
- When you are confident that you have measured the correct height, enter the height value.
- If a tree has more than one stem, measure the height for each stem.

h) field species identification

- If you know the species, indicate the species name and number of the reference collection. If you are not 100% sure, give a preliminary name and flag the species for specimen collection.
- Note: The correct name of the species is not important at this stage but it is extremely important that you correctly assign each tree to a species or morphospecies. Give each tree a name, either a real taxonomic name (e.g. Durio zibethinus), a fantasy name based on any conspicuous character (e.g. large leaves spiny), a local name (e.g. meranti) or a combination of both (e.g. Durio red bark or meranti small leaf). Each name represents one morphospecies. If you are sure (!!) that a tree belongs to an already existing morphospecies (i.e. one you have already given a name), use the same name (e.g. Durio red bark). If you are not completely sure, assign a new morphospecies by giving a new name (e.g. Durio red bark 2 or Durio red bigleaf).

- i) codes for data entry

Table 2. Code letters (left column) and descriptions (right column) used for data entry.

L	Stem leaning by more than 45°
Q	Stem broken above 1.3 m
I	Stem irregular where measured
R	Signs that there was an old break below 1.3 m
D	Dead tree
M	Missing tree (cannot be found)

3.2) Already censused individual or stem

If the tree individual or stem has a number tag, it has already been recorded in previous years.

- Check if the indicated position is correct
- Remeasure height and diameters
- Check species identification
- Enter all data into the KOBO App

➔ species identification:

Check whether the species indicated in previous inventories is correct. If correct, confirm the species name. If not, choose one of these options:

1.) If you are sure that you know the species, indicate the species name and the collection number of the reference collection (DMF0001-DMF0069).
2.) If you are not 100% sure, indicate a species name or field name and flag the tree for specimen collection.

3. Specimen and sample collection and functional trait analysis

Equipment

- Camera
- Secateurs
- Plastic bags
- Plastic tube
- Ethanol 40-50 %
- Paper tissue
- Labels
- Pencil
- Permanent marker
- Drying Oven
- Scale
- Scanner
- Paper envelopes
- Ruler
- Plant press with newspaper

Workflow

For all newly censused morpho-species, individuals are sampled for herbarium specimen, barcoding and functional trait analysis. Tree individuals in poor fitness condition (i.e. very few healthy leaves, with clear signs of plant disease, etc.) should not be sampled. If there is not enough plant material present to take all samples, prioritize sampling in the following order: 1. barcoding, 2. herbarium specimen, 3. functional traits samples.

Additionally, previously censused species with lacking data on functional traits are sampled (without herbarium specimen or barcoding collection).

4. DNA Barcoding

One individual of each newly censused morphospecies is selected. A leaf from this individual is cut and used for 2 identical barcoding samples.

In order to preserve the DNA present in leaf cells, the leaf must be dried rapidly. High levels of humidity may accelerate the process of DNA degradation. One of the best methods for drying leaf samples is using silica-gel. The silica-gel absorbs the moisture and keeps the samples dry. Silica gel containing a colour indicator changes its coloration when saturated with water.

- Select always fresh green leaves that do not show any sign of diseases.
- Cut a 2 x 3 cm piece of a leaf using scissors and wipe it with alcohol.
- Wipe the scissor to remove any remaining material before proceeding with the next sample.
- Place it in a plastic bag with silica gel.
- Label: plotID-treetag-bc written on a paper label inside the bag and with permanent marker on the outside of the plastic bag.
- Put all samples collected inside a plastic container. Keep samples always dry and protected from rain.
- Check on the sample every 12 hours and exchange the silica gel when necessary. The leaves must show a uniform coloration when dry.
- The used silica gel (only the silica gel!) can be dried in the oven to be reused. Place the silica gel over a tray and keep in the oven at 60 °C overnight (in case the oven reaches higher temperature, set the oven for 105 °C and let the silica gel dry for one hour).

5. Herbarium Specimen

- For all newly censused morphospecies, pictures are taken. Additionally, pictures are taken for one individual of the following species:

Trichospermum javanicum
Ficus aurata (leaves)

- Take pictures (ideally without flash or in dark background mode, see described below, so the colours look real) of the tree to document properties not shown in the specimen. Take pictures with and without a ruler.
    1. Tree tag and herbarium label next to each other
    2. Trunk base (lower 2 meters of the trunk) – e.g. buttresses, stilt roots, fluted trunk
    3. Trunk and crown (shooting upwards)
    4. Bark
    5. Bark slash and wood
    6. Tree habitus
    7. One branch with leaves (from both sides)
    8. Single leaves (from both sides)
    9. Detailed leaf base, margin, and tip (from both sides)
    10. Detailed petiole base incl. potential stipules and characteristics of young bark
    11. Two different branch tips (buds)
    12. Any conspicuous structures (e.g. dots on bark etc.)
    13. Fresh flowers
    14. Fresh fruits
    15. Cut fruits
- For camera settings, use either Macro mode (camera function – scene – macro), or produce black background, ideally in a shaded environment, in Manual mode (M) with:

  - ISO = 100 (small button on top)
  - aperture F = 11-16 (the higher the number the smaller the hole for incoming light)
  - the smallest possible time interval 1/1000 or 1/250
- Additionally, take notes regarding:

  - the colour of fruits and flowers at the time of collection
  - odour
  - sap (making a small cut in the bark)
- Branch not fertile (no flowers or fruits): take 2 duplicate specimens per tree
- Branch fertile (flowers or fruits present):

  take up to 8 duplicates for species that have not been collected yet,
  5 duplicates for species of which you already have good fertile material of the same type.

- Mark the branches with herbarium labels containing the collection number (acronym of first collector, e.g. VM or DMF, and running 4-digit number (one number per species per time of collection)) and the 4-digit tree tag.
- Place fertile specimens in separate plastic bags to protect them during transport.
- To dry the samples, place them in newspaper into a plant press. Remove some leaves that are on top of each other and turn some remaining leaves around to show both sides of the leaves.
- Place the plant press into the light drying oven and check on the samples at least every 24 hours and exchange newspapers if necessary.
- Place dry specimens covered in newspaper into a sealed plastic container with silica gel packages.
- Name the camera image files according to the scheme plot no._treetag_family_genus_species

6. Functional Traits

Samples for functional traits are collected:

1. If the individual belongs to **a new species** (not previously sampled).
2. If the individual was **not sampled in the last trait campaign** (Table 3)
3. If the individual belong to a species that **was undersampled** during the last sampling campaign, e.g., has only one sample (Table 4)
4. If the individual belongs to a planted species (Table 5)

Sampling design

1. **New species**

   Sample up to 3 individuals per plot and maximum of 15 individuals across plots.

2. **Individual not sampled**

   Sample this individual in cases it still alive and in good condition.

3. **Undersampled species**

   If you find individuals belonging to these species, sample up to 3 individuals per plot and a maximum of 15 individuals across plots.

4. **Planted species**

   Sample 5 individuals for each planted species (total = 30 individuals). For each species, aim at sampling individuals growing in different plots.

Table 3: Individuals not sampled during the last campaign.

plot	**treetag**	**fieldname**	**family**
45	14286	Cratoxylum cochichinense	Hypericaceae
29	11869	Urophyllum trifurcum (DMF0055)	Rubiaceae
35	12270	Neolamarckia cadamba (DMF0038)	Rubiaceae
7	14377	tree indet DMF0065 (DMF0065)	unknown
5	13392	Ficus glandulifera (DMF0016)	Moraceae

Table 4: Individuals with only one sample in the previous sampling campaign.

plot_ID	**tree_ID**	**species**	**height**
35	13992	Artocarpus dadah	-
45	14330	Urena lobata L. ssp. sinuata	3.25
19	13279	Secamone sp.DMF0064	6.35
34	13167	Secamone sp.DMF0064	11.2
45	14324	Secamone sp.DMF0064	7.1

Table 5: List of planted species.

Species code	**Species**
A	*Parkia speciosa*, fruittree
B	*Archidendron jiringa*, fruittree
C	*Durio zibethinus*, fruittree
D	*Dyera polyphylla*, timbertree
E	*Peronema canescens*, timbertree
F	*Rubrosshorea leprosula*, timbertree

Wood density

- Select one twig from the big branch. It should have a diameter of 1-2 cm (or smaller if no choice) and healthy-looking leaves.
- Cut 6-8 cm of the twig section that is reasonably straight and without branching.
- Place it in a plastic tube with 40-50% ethanol and label the tube (be careful with the ethanol that it does not remove the label writing). Alternatively (if fresh volume determined directly), use a labelled paper envelope instead.
- Label: plotID-treetag-wd
- Store the plastic tubes in a sealed plastic box and make sure there's always enough ethanol in the tubes.
- In the lab, estimate the volume of the twig using the water displacement method. Fill a container with water, place on a scale and calibrate to 0 g. Attach a needle to the wood sample. Sink the wood sample carefully into the water until it is covered completely in water. The sample should not contact the sides or bottom of the container. Read the mass in g on the balance. The measured weight of the displaced water is equal to the sample's volume (1 g H_2O = 1 cm^3).
- Oven-dry the sample at 70° C for 72 hours. Then, measure the dry weight on a scale.

Specific leaf area (SLA)

- Select one part of the big branch for the leaf sample. Choose 10 representative, fully-expanded (not very young and not very old) leaves and cut them off at the intersection between the petiole and the twig. If the leaves are compound, the leaflets are treated like leaves, so you cut 10 leaflets and leave the rachis and petiole as if they were twigs.
- Put them in a paper envelope or plastic bag and label. Put a second label on paper inside the bag just in case the writing outside on the plastic is removed.
- Label: plotID-treetag-lf
- Carefully wipe off any dirt of each leaf with paper tissue.
- Determine the total fresh weight (with 2 decimals) of 10 leaves, placing them in a plastic container on a scale after calibrating to 0 g.
- Scan the leaves in a horizontal way in a scanner together with a ruler, placing 5 leaves with the lower side up, and 5 leaves with the lower side down.
- If 10 leaves don't fit into the scanner altogether, conduct several scans, starting always with the biggest leaf. If one leaf is already to big, cut it into 2 or potentially more pieces, all scanned on their own.
- Name the scan files according to the following scheme:
  If all leaves of one sample fit in one scan, add -00: plotID-treetag-lf -00

If the leaves of one sample are distributed over 2 or more scans, add -01, -02, and so on: plotID-treetag-lf -01, plotID-treetag-lf -02, plotID-treetag-lf -03…
If at least one of the leaves of a sample has to be cut, each scan may only contain one leaf (or a part of it), never more than one. Give each leaf a letter (a, b, c, d, e) followed by a one digit-number of the leaf part. Here's an example:

  - plotID-treetag-lf -a1, plotID-treetag-lf -a2 for 2 scans containing cut parts of the first leaf
  - plotID-treetag-lf -b1 for the only scan of the 2nd leaf (can be entire or cut in the same scan)
  - plotID-treetag-lf -c1, plotID-treetag-lf -c2, plotID-treetag-lf -c3 for 3 scans containing parts of the 3rd leaf

- After scanning, store the leaves in a paper envelope including the paper label on the inside and also write the label on the outside of the envelope. Use one envelope per sampled individual (10 leaves). Place the envelope into the light drying oven.
- In the lab, dry the envelope containing the leaves at 70° C for 48 hours.
- Measure the total dry weight of the 10 leaves on a scale.

Appendix 2: Data processing protocol

All data processing has been performed in R version 4.4.1 (R Core Team, 2024).

For data cleaning of the 2024 dataset, specific data entry errors were corrected manually, including corrected data about recorded individuals' stems (mainstem vs. additional stem), species identity, tag types and tag numbers, specimen collection number, d10 values, number of stems for *Gigantochloa scortechinii* (bamboo) and information about stilt roots for *Leea javanica*. Duplicated data sheets of tree islands were removed, and zero values changed to NAs where applicable. All family names were added corresponding to the respective species names, as well as habitat, origin and life form information. Numbers of stems for *Gigantochloa scortechinii* (bamboo) were imputed when > 100 or when NA, and the variable was categorized into consecutive categories of 10 stems. Recorded non-woody species were removed from the data (Table 1). Further, NA species were excluded from the analysis.

For cross-year data cleaning of 2018-2024 and 2020-2024 datasets, importantly, all datasets of the respective years were harmonized and combined into cross-year datasets, allowing for adequate temporal comparisons of recruiting diversity. This included taking out dead and lost stems from the datasets, as well as all additional stems since only in 2024, additional stems were recorded. Moreover, in the 2018-2024 cross-year data, all liana species were removed as they were systematically only recorded in the 2024 dataset (Table 1). In the 2020-2024 cross-year dataset, only lianas with d10 > 1 cm were kept, to guarantee a consistent methodology (Table 1). After careful checks of tag numbers and exclusion of possible data entry errors, 24 stems were added to the 2022 data for which recordings in both 2018 and after 2022 were present, indicating specific data lacks for these stems in 2022. The manually added stems were indicated in the *filled_in_gap* columns of the data frames. Moreover, cross-year recorded stems that were detected in the field in 2024 to have vegetatively reproduced from main stems of planted trees of *Peronema canescens* were indicated in the datasets as no natural regeneration and later on removed.

Further, reidentifications of specific individuals were aligned across all years, as well as new species names adopted where species names generally changed. Unclear individual cases of *Ficus dimorpha* versus *Ficus variegata* were named *F. dimorpha* during data processing, as this seemed to be the much more abundant species across tree islands. For position data of stems, information on reference trees and oil palms was corrected, and x- and y-coordinates calculated from the position data for all stems. For cases where position data for the same individual differed between years, the latest available position data was applied to all recordings of the same individual across years. Further changes included removal of duplicates within one year, typos in tag numbers were corrected, old tag numbers matched with replaced tag numbers, and all stems were given an ID base matching with the collection number of their corresponding species.

The Excel sheet *Logbook data processing* in the R project folder lists all detailed changes made.

Table 1: List of removed species in different datasets.

Species	Data cleaning script	Reason for removal
2024 dataset		
Lygodium circinnatum (Burm.f.) Sw.	1	non-woody
Lygodium salicifolium_C.Presl	1	non-woody
Stenochlaena palustris (Burm.f.) Bedd.	1	non-woody
Dioscorea hispida Dennst.	2	non-woody
Mikania micrantha Kunth.	2	pot. non-woody (species not recorded 2018-2022 although present)
Chromolaena odorata (L.) R.M.King & H.Rob.	2	pot. non-woody (species not recorded 2018-2022 although present)
Cross-year 2018-2024 dataset		
Lygodium circinnatum (Burm.f.) Sw.	1	non-woody
Lygodium salicifolium_C.Presl	1	non-woody
Stenochlaena palustris (Burm.f.) Bedd.	1	non-woody
Dioscorea hispida Dennst.	2	non-woody
Mikania micrantha Kunth.	2	pot. non-woody (species not recorded 2018-2022 although present)

Chromolaena odorata (L.) R.M.King & H.Rob.	2	pot. non-woody (species not recorded 2018-2022 although present)
Bonamia semidigyna (Roxb.) Hallier f.	2	lianas not recorded in 2018
Bridelia cinnamomea Hook.f.	2	lianas not recorded in 2018
Calopogonium mucunoides Desv.	2	lianas not recorded in 2018
Camonea pilosa (Houtt.) A.R.Simões & Staples	2	lianas not recorded in 2018
Centrosema molle Mart. ex Benth.	2	lianas not recorded in 2018
Chonemorpha verrucosa (Blume) D.J.Middleton	2	lianas not recorded in 2018
Combretum cf. sundaicum Miq.	2	lianas not recorded in 2018
Coptosapelta cf. tomentosa (Blume) Valeton ex K.Heyne	2	lianas not recorded in 2018
Derris amoena Benth.	2	lianas not recorded in 2018
Erycibe rheedei Blume	2	lianas not recorded in 2018
Macrolenes cf. dimorpha (Craib) J.F.Maxwell	2	lianas not recorded in 2018
Maesa sumatrana Scheff.	2	lianas not recorded in 2018
Millettia sericea (Vent.) Wight & Arn. ex Hassk.	2	lianas not recorded in 2018
Mucuna biplicata Teijsm. & Binn. ex Kurz	2	lianas not recorded in 2018
Mussaenda frondosa L.	2	lianas not recorded in 2018
Phanera semibifida (Roxb.) Benth.	2	lianas not recorded in 2018
Reissantia cassinoides (DC.) Ding Hou	2	lianas not recorded in 2018

Secamone sp.KR5266	2	lianas not recorded in 2018
Stixis scortechinii (King) M.Jacobs	2	lianas not recorded in 2018
Tetracera scandens (L.) Merr.	2	lianas not recorded in 2018
Tetrastigma coriaceum (DC.) Gagnep.	2	lianas not recorded in 2018
Uncaria attenuata Korth.	2	lianas not recorded in 2018
Uncaria cordata (Lour.) Merr.	2	lianas not recorded in 2018
Uvaria cf. grandiflora Roxb. ex Hornem.	2	lianas not recorded in 2018
Mezoneuron sumatranum (Roxb.) Wight & Arn. ex Voigt	2	lianas not recorded in 2018
Arcangelisia flava (L.) Merr.	2	lianas not recorded in 2018
Gnetum tenuifolium Ridl.	2	lianas not recorded in 2018
Jasminum elongatum (P.J.Bergius) Willd.	2	lianas not recorded in 2018
Cross-year 2020-2024 dataset		
Calopogonium mucunoides Desv.	2	lianas d10<1 cm (not recorded in 2020 and 2022)
Arcangelisia flava (L.) Merr.	2	lianas d10<1 cm (not recorded in 2020 and 2022)
Gnetum tenuifolium Ridl.	2	lianas d10<1 cm (not recorded in 2020 and 2022)
Callicarpa pentandra Roxb.	-	automatically dropped out as not present in 2020-2024, only in 2018
Ficus grossularioides Burm.f.	-	automatically dropped out as not present in 2020-2024, only in 2018
Trichospermum javanicum Blume	-	automatically dropped out as not present in 2020-2024, only in 2018

Macaranga hosei King ex Hook.f.	-	automatically dropped out as not present in 2020-2024, only in 2018
Lygodium circinnatum (Burm.f.) Sw.	1	non-woody
Lygodium salicifolium_C.Presl	1	non-woody
Stenochlaena palustris (Burm.f.) Bedd.	1	non-woody
Dioscorea hispida Dennst.	2	non-woody
Mikania micrantha Kunth.	2	pot. non-woody (species not recorded 2018-2022 although present)
Chromolaena odorata (L.) R.M.King & H.Rob.	2	pot. non-woody (species not recorded 2018-2022 although present)

Appendix 3: Declaration of independent work

GEORG-AUGUST-UNIVERSITÄT
GÖTTINGEN

Master of International Nature Conservation, Goettingen University

Selbständigkeitserklärung

Ich versichere hiermit, dass ich die vorliegende Arbeit ohne fremde Hilfe selbstständig verfasst und nur die von mir angegebenen Quellen und Hilfsmittel verwendet habe.
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Declaration of independent work

I hereby declare that I have produced this work independently and without outside assistance, and have used only the sources and tools stated.
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I am aware that failure to comply with these principles will result in the examination being graded "Nicht bestanden", i.e. failed.

Place/date Göttingen/15 Dec 2025 Name Vivien Michel

Signature Michel